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NEW EVIDENCE ON THE ORIGIN OF MAIZE*

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The origin of maize is unknown. No wild species has yet been discovered that can be said with certainty to represent the ancestral form from which cultivated maize originated. *Euchlaena mexicana* Schrad. is the closest known relative of maize, and competent geneticists have held the view that a few large scale mutations could have transformed such a plant into the prototype of Indian maize. But the studies of Mangelsdorf (1947) and Rogers (1950) in recent years have shown that many small differences distinguish existing forms of teosinte and maize. However, no one knows how many of the gene differences that separate maize and teosinte at the present time have appeared by mutation in the thousands of years since the wild maize plant began to be cultivated by early Americans. It is well known that collections of teosinte from different localities are genetically very different. To what extent these differences are due to admixture with different types of maize or to relatively high mutation rates for various genes can only be conjectured. It is quite possible that the progenitor of teosinte was a more valuable food plant and more directly in the evolutionary line of primitive maize than existing forms of teosinte.

There is at present no general agreement among students of the problem, concerning either the interrelations of maize and its wild relatives or the place where maize originated. In fact there is far from unanimous agreement as to the continent or even the hemisphere where the progenitor of maize was indigenous. Like many other subjects about which little is definitely known there has been much wild speculation and much has been written about the evolutionary history of maize as a cultivated plant.

To review adequately the literature of this subject would require more time than is available for this talk. I have chosen rather to enumerate some of the more important known facts about the present center of di-

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versity of the American Maydeae, their cytological characteristics, the crossability of existing types of maize and Tripsacum in Mexico and Guatemala, and contributions of archeology during the last decade that have thrown much light on the early history of maize culture.

Even with a subject as controversial as this there probably is general agreement that the present center of diversity of the American Maydeae is in Mexico and Central America. Teosinte occurs only in this region, where the annual diploid form is especially abundant in the Cuchu Matanes Mountains of northwestern Guatemala just south of the Mexican border and in the state of Guerrero of southern Mexico. Having explored both of these regions extensively during the past five years I am inclined to agree with my Mexican colleague, Efraim Hernandez-Xolocotzi, that more of the annual teosinte is growing over a wider area at the present time in southern Mexico than in Guatemala. The tetraploid teosinte, *Euchlaena perennis* Hitchc., was collected in western Mexico at Guzman by Hitchcock in 1919, but has now disappeared from the type locality. Teosinte has never been reported from South America.

At least a half dozen species of Tripsacum are known from Mexico, including both diploids and tetraploids, and in addition there are many local tetraploid populations, apparently of amphidiploid origin either from the recently discovered diploids, *T. maizar* Hern. et Rand. and *T. zopilotense* Hern. et Rand. (Hernandes and Randolph, 1950), or similar species. At the periphery of the genus in northern South America is found *T. australe* Cutler et Anderson, a diploid species similar to *T. dactyloides* L., which is widely distributed in the southern and eastern United States at the northern limit of the range of the genus.

In addition to teosinte and Tripsacum there are in Mexico and neighboring areas of Central America and the United States many different kinds of cultivated maize, of which numerous races that have been identified in Mexico are to be described by Dr. Wellhausen. Whether there are in existence at the present time in this region more or fewer types of maize than there are in the highlands of Peru and Bolivia has not been definitely determined, but it is certainly true that there are many kinds in both regions, and the archeological evidence of the spread of primitive cultures into South America from the north obviates the necessity of assuming an independent origin of cultivated maize in each of these areas.

Recognition of the significance of the distribution of the American Maydeae in relation to the problem of the origin of maize has been followed in recent years by important discoveries in Mexico, Guatemala and the southwestern United States that furnish strong support for the view that maize originated in this area rather than in South America.

Although the present center of diversity of the Maydeae is south of the border between the United States and Mexico, there is a very definite possibility that it might have been much farther north during the early post-glacial period when subtropical floras and a humid climate extended northward beyond their present limits. In fact, the existence of a sizable

group of Maydeae in southern Asia as well as in Central America suggests that there was a post-glacial southward migration of the Maydeae along both sides of the Pacific from a common ancestral homeland in the region of the Bering Straits. There is support for this possibility in the fact that it is now generally conceded by ethnologists, such as Roberts (1951) and Solecki (1951) of the Bureau of American Ethnology, that early man first came to the Americas from Asia by way of the Bering Straits, and that Folsom man is now known to have inhabited vast areas in the southwestern United States from 10,000 to 5,000 years ago, a period of vital importance to students of the early history of maize culture. Since Folsom man was a hunter, roaming in nomadic tribes searching for food, and there is as yet no evidence of sedentary tribes dependent on agriculture and cultivated plants for food earlier than three or four thousand years ago, it seems improbable that maize was brought to the Americas from Asia across the Bering Straits, certainly not by Folsom man or his descendants, unless at an appreciably later date. However, it would seem unwise in the present imperfect state of our knowledge to label as "utter nonsense" the views of Stonor and Anderson (1949) concerning the possibility of an Asiatic origin of maize.

The origin of cultivated plants, according to Vavilov, should be sought in the region of the greatest diversity of existing cultivated forms and near the center of distribution of the most closely related wild species. To these two rules should be added Matthews' generalization that centers of origin may be expected to correspond to the area occupied by the most advanced species, with the more primitive species occupying the periphery of the range of distribution of the genera concerned. These basic concepts of Vavilov and Matthews with minor variations to make allowance for possible shifts in centers of diversity, have been very useful in identifying the place of origin and the wild species from which most of our more important crop plants have originated. They have also been useful in directing the search for the origin of maize to the region in Mexico where diploid ancestral types of Tripsacum are persisting as relic species along with more highly evolved polyploid forms of both Tripsacum and teosinte.

EXPERIMENTAL EVIDENCE

During four consecutive years from 1946 to 1949 tests were conducted in Mexico and Guatemala of the crossability of native races of maize and tetraploid Tripsacum. Crosses were attempted between 44 races of maize as the seed parent and 20 different kinds of Tripsacum from various localities, which are indicated in table 1.[1] No viable seeds were obtained from the 132,000 maize gametes tested in 65 combinations. One of the combinations, a Celaya synthetic maize hybrid developed by Dr. Wellhausen of the Rockefeller Foundation in Mexico, that was pollinated by a tetraploid Tripsacum from Acahuizotla, Mexico, produced immature embryos from which two

[1]These experiments were fully described in a paper presented at the Seventh International Botanical Congress held at Stockholm, Sweden, in July, 1950, to be published elsewhere.

TABLE 1

CROSSABILITY OF MEXICAN AND GUATEMALAN TRIPSACUM AND MAIZE

	Varieties and species tested		Comb. tested	Maize ears pol.	Maize gametes tested
	Maize	Tripsacum			
Corn × 4n Tripsacum					
Guatemala, 1946					
Finca Barcena, Antigua	3	1	3	152	29,450
Mexico, 1947					
Puente Grande, Tequila, Chapingo	5	5	8	140	27,350
Mexico, 1948					
Jalostoc	7	1	7	28	450
Mexico, 1949					
Progreso	12	11	30	129	44,430
Corn × 2n Tripsacum maizar					
Mexico, 1948					
Jalostoc	6	1	6	80	1,300
Mexico, 1949					
Progreso	5	1	5	35	14,160
Corn × 2n Tripsacum zopilotense					
Mexico, 1949					
Progreso	6	1	6	48	14,870
Totals	44	21	65	612	132,010

hybrid seedlings were obtained by excising and culturing the embryos on a sterile nutrient agar. The defective grains containing these partly developed embryos would not have been viable under natural conditions.

The results of these very extensive crossing experiments do not support the concept of the hybrid nature of teosinte and modern maize contained in the tripartite hypothesis advanced by Mangelsdorf and Reeves in 1939 to account for the origin of maize. As restated briefly by Mangelsdorf and Cameron (1942) this hypothesis assumed: "(1) that cultivated maize originated from a wild form of pod corn which was once, and perhaps still is, indigenous to the lowlands of South America; (2) that Euchlaena (teosinte), the closest relative of maize, is a recent product of the natural hybridization of Zea and Tripsacum which occurred after cultivated maize had been introduced by man into Central America; (3) that new types of maize originating directly or indirectly from this cross and exhibiting admixture with Tripsacum comprise the majority of Central and North American varieties." If there has been any appreciable amount of natural crossing of Tripsacum and maize in their native habitats in these areas it must have occurred at a much earlier period before the present level of genetic cross incompatibility became established in the numerous widely separated Tripsacum populations which are at present effectively isolated by extensive geographic barriers.

It is not necessary to postulate hybridization of Tripsacum and Zea to account for the "tripsacoid" characteristics of existing varieties of

maize. Related species that have had a common origin must have many genes in common, with probably not more than a very small per cent of the total being concerned with species delimitation. Under domestication, characters that enhanced the food value of primitive maize, such as increased kernel size and row munber, would have high selective value and be retained in improved varieties, while others of negligible selective value, including the shape of the ear, texture of glumes and number of tassel branches ordinarily would be expected to persist in certain varieties but not in others.

The experimental evidence that Mexican and Guatemalan Tripsacum and maize are highly cross sterile and the discovery of the maize-like species, *Tripsacum maizar,* in Southern Mexico by Hernandez and Randolph (1950) have added substantial support to the theory of the independent origin of maize, Tripsacum and teosinte from a common ancestral form, as first advocated by Montgomery nearly 50 years ago and ably supported by Weatherwax more recently (1935, 1950). They suggest that the importance of intergeneric hybrids in the evolution of cultivated maize has been overemphasized.

CYTOLOGICAL EVIDENCE

There is very definite cytological evidence that no significant amount of intercrossing of Tripsacum and maize has occurred in recent times, and probably not for many centuries. There are very distinct numerical and morphological differences between the chromosomes of the two genera that intercrossing would have eliminated. All known species of diploid Tripsacum have a gametic chromosome number of 18; corn has a gametic number of 10. Different base numbers such as these would not be expected to prevail in species that produce fertile hybrids with any significant frequency under natural conditions. The same is true of the very pronounced differences in chromosome morphology that distinguish the two genera.

It is a curious fact that the proponents of the view that there have been significant amounts of admixture of Tripsacum and maize gemplasm in Central America in recent times, and that teosinte originated as a Tripsacum-Zea hybrid, apparently have not fully appreciated the significance of the very conspicuous differences other than knob relationships, existing between the chromosomes of these genera as described by Longley (1937). It is inconceivable that maize and Tripsacum could have retained such pronounced differences in chromosome number and morphology while occupying the same areas, if they were producing fertile hybrids and exchanging chromosome segments with any appreciable frequency.

There has been much speculation about the possibility that the characteristic knobs of maize chromosomes were derived from Tripsacum. Many varieties of maize have fairly numerous intercalary, and occasionally terminal knobs. *Tripsacum dactyloides* and *T. floridanum* Porter have terminal knobs on most of their chromosomes. Just how the knobs were transferred from their terminal position in Tripsacum to intercalary regions

of the maize chromosomes is not known. Since the unbroken, terminal ends of chromosomes ordinarily do not fuse with broken ends of the same or other chromosomes something other than typical translocations must be postulated to explain the transposition of terminal Tripsacum knobs to intercalary regions of the maize chromosomes. It is possible as Longley has suggested that knob positions are subject to gene control, but experimental evidence of this is lacking.

The argument that the presence of knobs in maize is evidence of Tripsacum contamination is of questionable value since it has been demonstrated that Tripsacum and maize of the regions where it has been assumed that hybridization has occurred in recent times are highly cross sterile. Also, Tripsacum species devoid of knobs are now known from both South America and Mexico. *Tripsacum maizar,* a Mexican species, which has a closer resemblance to maize than any other known species of Tripsacum, is essentially devoid of knobs and the same is true of the more grass-like *T. australe* of South America (Graner and Addison, 1944). Furthermore, Tripsacum is either very rare or nonexistent in regions such as the San Antonio Huixta area in northwestern Guatemala that have been cited as outstanding examples of Tripsacum introgression (Mangelsdorf and Cameron, 1942). Varieties of maize and teosinte with numerous terminal knobs are especially prevalent but no Tripsacum was encountered by the writer during five days of exploration of this region in 1946, except at higher altitudes where the native Indian maize has few knobs and there is no teosinte. It is possible that knob numbers were variable among the ancestral Maydeae from which existing genera evolved, or a reduction in number occurred subsequently in certain evolutionary lines originating from a common ancestral stock with numerous knobs, or knobs may have evolved in some lines and not in others that were derived from a knobless ancestral form.

The subject of chromosome number and morphology in the Maydeae should not be dismissed without further reference to the relation of Euchlaena to Zea and Tripsacum, especially as the hypothesis of the origin of Euchlaena as a hybrid of Tripsacum and Zea, originally advanced by Mangelsdorf and Reeves in 1939, continues to be advocated by its sponsors. In considering the possible evolutionary significance of Zea-Tripsacum hybrids it should be borne in mind that the F_1 progeny of the diploid forms of maize and Tripsacum have 28 chromosomes and are completely sterile except for the functioning of occasional unreduced gametes in backcrosses to maize. The hybrid plants of this second generation have 38 chromosomes including a haploid set of 18 Tripsacum chromosomes and two haploid sets of maize chromosomes. They are partly fertile and produce gametes having a complete haploid set of 10 maize chromosomes and from one to 18 Tripsacum chromosomes. It is only from repeated outcrossing of such 38 chromosome plants to maize, or the selfing of the third and fourth generation backcrossed progeny of the original cross, that individuals with 20 chromosomes, the number prevailing in diploid species of Euchlaena, are obtained. Such 20-chromosome plants are with rare exceptions pure maize, having

chromosomes unaltered by their association with the Tripsacum chromosomes. The exceptions have to be scrutinized very carefully to detect any trace of Tripsacum germplasm, a result which confirms the cytological evidence that there is very little crossing over between the chromosomes of maize and Tripsacum.

It was demonstrated very conclusively by Longley (1937) that the 10 pachytene chromosomes of maize and teosinte are very similar in length and in arm ratios. In this same paper Longley also published a figure showing very clearly that the 18 chromosomes of Tripsacum have a much shorter average length than the maize and teosinte chromosomes, and they also have very different arm ratios. With respect to chromosome number, length and arm ratios, teosinte is so similar to maize and so different from Tripsacum that the possibility of a hybrid origin of teosinte, suggested by Mangelsdorf and Reeves, can be dismissed without further consideration on the basis of the cytological evidence alone.

Teosinte differs sufficiently from maize, especially in the nature of the distichous pistillate spikes and the manner in which the seeds are borne individually in sunken cavities of the rachis and partly enclosed by coriaceous glumes, to be deserving of the separate generic status given it by taxonomists. Although teosinte can be crossed with maize without difficulty, when the two species are growing together as they commonly are in Mexico and Guatemala there is as previously stated relatively little natural crossing and teosinte retains its individuality to a remarkable degree.

EVALUATION OF ARCHEOLOGICAL EVIDENCE

Archeological discoveries in recent years have made important contributions to existing knowledge of primitive maize. Well preserved cobs and kernels were discovered at Bat Cave, New Mexico, in 1948 by an expedition of the Peabody Museum of Harvard University of which Herbert W. Dick, a graduate student in anthropology at Harvard, was the leader and C. Earle Smith, Jr., an undergraduate, was the botanist; the cobs were subsequently described by Mangelsdorf and Smith (1949). These remains furnish conclusive evidence that a small-eared type of maize was being used for food in the southern United States approximately 3,000 years ago. The oldest sample of which sufficient material was available for dating with the radioactive carbon technique of Arnold and Libby (1951) was found by them to be 2,249 ± 200 years old; the earlier date of 4,000 years given by Mangelsdorf for the oldest specimens at the bottom of the cave was obtained by extrapolation.

Similar but less well-publicized remains of prehistoric maize were found in 1943 at Arica, Chile, by Junius Bird, archeologist of the Museum of Natural History in New York. The beautifully preserved cobs from Chile are very similar in general appearance to those from Bat Cave, which probably antedate them by several centuries at least. Later explorations under Dr. Bird's leadership at Huaca Prieta in the Chicama Valley of

Southern Peru revealed the existence there of a very early prehistoric culture based on a primitive type of agriculture that included such plants as beans, chili peppers, squash, gourds and cotton, but in which maize was conspicuous by its absence (Bird, 1948). The subsequent appearance of maize in this area was found by Bird to have coincided with the arrival of Cupisnique pottery from the north, which occurred 2,665 ± 200 years ago according to Arnold and Libby (1951). With the aid of the radioactive carbon technique used to establish this date these same authors estimated that the earliest Bat Cave specimens were aged 3,000 to 3,500 years. Thus these archeological data indicate very definitely that cultivated maize existed at an appreciably earlier period in the southwestern United States than in South America and add strong confirmation to the view that maize originated near the present center of diversity of the American Maydeae in Mexico and Guatemala.

The Bat Cave and Chilean cobs are very well preserved and afford direct proof of the existence at that very early period of a plant with highly specialized ears of edible grain. The complexity of the ears is comparable to that of modern maize, indicating that the plant had already been grown under cultivation for many centuries; without adequate means of seed dispersal such a plant has little or no survival value in nature. The cobs of the oldest specimens are from two to three inches in length and have from eight to sixteen rows of closely packed kernels somewhat smaller than those of existing varieties of pop corn; in fact they must have been about the same size as the kernels of teosinte, but without the horny glumes of teosinte.

None of these prehistoric cobs had elongate husk-like glumes enclosing individual kernels as in typical pod corn. Their glumes were in fact no more conspicuous than those of numerous modern varieties of maize; certainly the kernels could be readily shelled for grain or eaten in the fresh condition directly from the cob as the Indians of the Americas are accustomed to do at the present time. It is difficult to see in these specimens of the most ancient cultivated maize thus far discovered, or in the existing wild relatives of maize, any support for the hypothesis that maize originated from a primitive type of pod corn of the sort that is known to be controlled by the dominant *Tu* allele in chromosome 4 of maize.[2]

SUMMARY AND CONCLUSIONS

Conclusions to be drawn from the recent evidence relating to the origin of maize may be helpful in directing future investigations of this problem. In conducting a piece of research it is often helpful to outline tentative

[2]A brief description of specimens of a very ancient type of maize considered to be the oldest yet discovered, which resemble pod corn more closely than any previously described, was published by Hugh C. Cutler in the February, 1951, issue of the Chicago History Museum Bulletin. More information is needed to evaluate the importance of this discovery.

working hypotheses to serve as guides during the progress of the investigation. Botanical and archeological research of the past decade has made substantial contributions to existing knowledge of the evolutionary history of maize, and various hypotheses formulated in past years are now in need of revision.

At some remote period following the migration of Folsom man from Asia to North America from 5,000 to 10,000 years ago, the nomadic tribes that spread southward through the United States into Mexico and Central America assumed a more sedentary way of life and became dependent for food and clothing on a primitive type of agriculture. These early Americans discovered wild plants that were suitable for food. Various cucurbits, beans and primitive maize were most certainly among the food plants cultivated by the first farmers of the Americas; but the place and time of domestication of these plants is unknown. With respect to maize it now appears that the time of domestication was from five to ten thousand years ago. The place was most probably in Mexico or the southwestern United States where a humid subtropical climate apparently flourished during that period. It may be assumed that the progenitor of cultivated maize was intermediate in most of its characteristics between the maize of the Bat Cave era and its closest relatives, Euchlaena and Tripsacum. Substantial progress in the solution of the intriguing problem of the origin of cultivated maize may be expected from further archeological and botanical studies of unexplored areas of the southwestern United States and Mexico.[3]

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[3]Since this was written the writer had an opportunity through the kindness of Dr. Paul C. Mangelsdorf, Director of the Botanical Museum of Harvard University, to examine the Bat Cave cobs and was particularly impressed by the resemblance to teosinte of specimens of the oldest cobs, especially with respect to their size and slender rachis, the manner in which the very small seeds are deeply sunken in the ear and protected by a thick outer glume as in Euchlaena and Tripsacum. The glumes of these primitive ears are not as horny as those of Euchlaena and Tripsacum; they are fleshy and not membranaceous as in typical pod corn. The Bat Cave ears differ from those of Euchlaena in having paired spikelets and in being polystichous rather than distichous.

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SELECTIVE PROCESSES IN THE DIFFERENTIAL FERTILITY OF FAMILY STOCKS

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Among the people of Western Europe, and those of Western European descent in the United States, Canada and elsewhere, only about ten per cent of the children born alive now die before the midpoint of their reproductive period. In this narrow field in which death-selection operates, deaths occur usually from natural causes, and too early for weaknesses in intelligence or personality to have been contributing factors. Death no longer plays a significant part in the selection of the mental and emotional traits which will survive from one generation to another.

Births among Western European peoples, though also greatly reduced in number, vary throughout the whole population. Some people having large families, and some small, selection has a wide field in which to operate. Much of this variation in size of family in the United States today occurs for one or another of two reasons. First because varying proportions of people practice contraception. Second, because an increasing number of American couples limit the size of their families and space their children according to plan, and among such couples, size of family is a wholly voluntary matter, determined by the reaction of individual personalities to the psychological pressures of their environment. Among these couples, variations in births provide a framework in which selection may be much affected by differences in the mental and emotional qualities of individuals.

Thus we see selective processes operating in the world today in three quite different settings; of which one or another provides the major background for selection in a particular geographical area or among a particular group of people.

Under the first type of process, still prevalent in the non-European world, survival will go, in the words of Dobzhansky (1951) to those people who are stronger, more resistant, live longer, are more sexually active, or more fecund. This is the type of selection which has gone on in all times past, with all living things: Darwin named it natural selection.

The second type of selective process includes the majority of human groups of Western European descent. Among these groups the forces of death selection have become secondary to the selection which takes place in the framework of social processes which determine who shall have access to contraception, and which determine variations in the effectiveness of contraception. The major forces of selection are still those of chance, but the chance is determined by social conditions which are or can be under human control; we might call this social selection.

The third and perhaps final process of selection is at present the major force only among those limited groups of people who are able to, and actually do, plan the number and spacing of their children. Here selection operates in the framework of voluntary personal decisions, psychologically determined. This might be called psychological selection, or individual, or voluntary selection.

This latter process of selection is of particular interest because there is a long-term continuous trend toward increasing the proportionate numbers of this group of family-planning people; and if, as seems likely, there is developed some new and effective means of interrupting fertility by inoculation or medication, this group would probably grow rapidly to comprise the entire population of the United States and eventually of the world.

SOCIAL AND PSYCHOLOGICAL FACTORS AFFECTING FERTILITY

The scientific study of social and psychological factors affecting fertility is very recent.

Galton in "Hereditary Genius (1950 ed)" pointed out the importance of social factors in selection. He noted that size of family varied inversely with age at marriage, and noted the dying out of family lines through the marriage of able and ambitious men to heiresses whom he thought were of relatively sterile stocks.

In the United States, Flanagan (1942) using modern techniques, made a study of psychological factors as they effect variations in births among army aviators. It was the first study of its kind and laid some of the groundwork for a larger study made in Indianapolis in 1941, which was to include both social and psychological factors.

The Indianapolis Study was organized during 1938–40 by a group which included psychologists, demographers, and a leading medical statistician. It was based on a preliminary house-to-house canvass and a subsequent intensive study involving personal interviews, and the filling out of carefully prepared and pretested schedules and questionnaires. Twenty-three hypotheses were laid down which it was hoped might be wholly or partially proved or disproved. The analysis of the material bearing on these hypotheses is now nearing completion with publication in current issues of the *Milbank Memorial Fund Quarterly*. It is material which papers on differential fertility will draw on heavily for years to come (cf. Kiser et al, 1943–1951).

Two types of data were collected in the Indianapolis Study; the first from the Household Survey, covering the 41,594 native-white couples, wife under 45 years of age, neither ever divorced, found in the city's 102,877 dwelling units of white families, all of which were visited by the canvassers; this group may be considered typical of the people in any fair-sized American city. The second from the final Interview Group, covering data for an adjusted and inflated sample of 1,444 "relatively fecund" and 533 "relatively sterile" couples selected on the basis that they were married in 1927, 1928, or 1929 with wife under 30 and husband under 40 at time of marriage, both

native white, both Protestant, both having completed eighth grade, and both with at least eight years of residence in a large city since their marriage; this group may be considered typical of the people who practice family limitation in a fair-sized American city; it was further subdivided according to the extent and effectiveness of their practice of contraception.

It is now possible to draw at least a few generalizations which apply to the social and psychological processes of selection. They are as follows:

In an American city, fertility is more influenced by contraception than by impairment of fecundity. Contrary to the views frequently expressed in the past, differences in size of family in the United States are chiefly the result of differences in the use of some means of preventing conception. In the Indianapolis Interview Group, fecundity, that is, the physical capacity to reproduce, is estimated at 5,265 possible pregnancies, and 4,594 possible births per 1,000 couples during the twelve to fifteen years from marriage to interview. This figure for the number of children who would have been born if there had been no use of contraceptives is 27.4 per cent lower than the medium estimate of what the rate would have been if there had been no defects in the reproductive system which reduced the number of conceptions or increased the time required for conception. Taking into account the actual practice of contraception among the couples studied, it appears that defects in the reproductive system lowered fertility 21.3, 18.1, and 13.3 per cent, respectively, under three assumptions of high, medium, and low fecundity. On the other hand, under these same assumptions of high, medium, and low fecundity, voluntary control reduced the birth rate by 72.2, 67.2, and 64.4 per cent, respectively. In this selected urban group, there was still an inevitable weeding out of infertile stocks, but there was an even larger weeding out of stocks who under the circumstances intentionally limited their fertility (Kiser and Whelpton, 340–341).

Age at marriage is an important factor in all three types of selection: Galton, quoting figures obtained for 1871 from the Lying-in-Hospital of St. Georges-in-East, gives the data in table 1 (Galton, 1951, p. 209).

TABLE 1

Age of mother at marriage	Average fertility
15–19	9.12
20–24	7.92
25–29	6.30
30–34	4.60

At the time of this study, contraception was almost unknown, and birth rates were high. Of English wives, married 1861–1871 (age at marriage standardized on upper class American series), over 56 per cent had five or more children (Lorimer and Osborn, 1934).

In the Indianapolis Study, the fertility of the Interview Group (inflated sample), interviewed twelve to fifteen years after marriage, and

TABLE 2

FERTILITY RATES BY AGE AND AGE AT MARRIAGE

Age of wife		Number of wives	Children ever born per 100 wives	
At marriage	At interview	Indianapolis interview groups	1940 Census cities 250,000+	Indianapolis interview groups
Under 18	25–29	218	232	205
Under 18	30–34	155	292	243
18–19	30–34	500	219	178
20–21	30–34	381	175	170
20–21	35–39	60	210	140
22–24	30–34	70	137	127
22–24	35–39	381	174	140
25–26	35–39	121	132	125
25–26	40–44	20	162	145
27–29	40–44	62	142	73

compared to the figures from the 1940 census for cities of 250,000, is shown in table 2.

The Interview Group in the Indianapolis Study, most of whom used contraception, show greater variations in size of family by age at marriage than the population at large, a smaller proportion of whom used contraception; and both show greater variations than Galton's group, of whom probably very few used contraception.

If, as seems likely, trends in the country as a whole ultimately follow the example set by the group in Indianapolis most of whom practiced contraception, then age at marriage will be an increasingly important factor in determining who shall survive.

A sense of economic insecurity reduces the size of planned families: In the United States, as in most other countries, there is a direct relationship between socio-economic status and the use and effectiveness of contraception. This is quite sufficient to account for the large differences in rates of reproduction between city and country and between different socio-economic classes, which were so frequently misinterpreted by the early eugenists. Present differences in contraceptive practice are also sufficient to account for the large differences in rates of reproduction between different countries, which are the despair of our present-day Point Four planners. We assume that the world-wide trend toward an increasing use of contraception will continue, and that a cheap and fully effective contraceptive will probably be developed and generally accepted before present transitory conditions have had any great effect on the distribution of genes. We are therefore particularly interested in what we have called the third or final process in which selection takes place, that in which couples plan the number and spacing of their children, and a major part is played by psychological factors.

The Indianapolis Study throws light on this subject for the first time. The 1,444 "relatively fecund" couples in the "inflated survey group" were used to test the hypothesis: "The greater the feeling of economic insecurity, the higher the proportion of couples practicing contraception effectively and the smaller the planned families." The first part of the hypothesis is not borne out by the data, but the second part of the hypothesis is supported. The size of "number-and-spacing-planned" families is directly associated with economic security regardless of differences in socio-economic status (Kiser and Whelpton, 1951).

Six items relating to wives and husbands separately were used to form an index of economic security of the couple. One of them was the interviewer's direct rating, and five were self-ratings of each spouse on questions designed to be indicative of feeling of economic security. Among the "number-and-spacing-planned" families the relation between the index of economic security and number of children is shown in table 3:

TABLE 3*

Index of economic security	Children ever born per 100 couples		Per Cent childless
	All couples	Fertile couples	
90+	188	213	11.8
80-89	107	134	20.0
70-79	130	167	21.9
60-69	99	145	31.9
Under 60	57	135	57.4

*The number of couples is too small for statistical validity, but the table is consistent with previous studies which have shown an increase in size of family at higher rent levels.

There is a remarkable increase in childlessness as economic security declines; but even among those couples who were not childless, those at the top in economic security had almost twice as many children as did those at the bottom. It appears from the study that the positive relationship between a sense of economic security and size of family among people who plan the number and spacing of their children holds regardless of differences in socio-economic status. The picture is all the more striking because there is no evidence that any larger proportion of people planned and spaced their children because of their sense of economic insecurity. In fact fertility-planning status was directly related to feeling of economic security, albeit this type of relationship appeared to stem almost entirely from a positive relation of socio-economic status to both economic security and fertility planning. The couples who planned and spaced their children were definitely not more affected by adverse economic factors than were those who did not bother to plan and space their children.

In a separate study of fertility planning and fertility rates by socio-economic status, the Indianapolis Study gives further evidence of the reversal of class differentials in fertility among couples who use contraception effectively. Of the 1,444 "relatively fecund couples" in the ad-

TABLE 4

Husband's average annual earnings since marriage	Number of couples	No. of children per 100 couples
$3,000 and over	55	149
$2,000–$2,999	94	128
$1,600–$1,999	86	91
$1,200–$1,599	123	97
Under $1,200	44	68

justed sample, 382 successfully planned and spaced the number of their children. Their fertility in relation to the husband's annual average earnings since marriage is shown in table 4.

Even at those relatively low annual earnings, the better-off—and therefore the more secure couples—had more than twice as many children as those with the smallest incomes. It is interesting to note that their fertility rates, taking place under what we have called the third or psychological process of selection, are the inverse of the rates for socio-economic classes so long reported under the second or social process under which most selection is operating today.

The relative importance of contraception as compared to impairments of fertility, the importance of age at marriage, and the effect of a feeling of economic insecurity seem to be the only factors in regard to which it is possible to draw broad generalizations on the basis of present knowledge. If, as we believe, we are moving rapidly toward the time when the use of contraception will be almost universal in the United States and will be almost wholly effective, class differences in fertility are likely to be absorbed by factors such as age at marriage, economic security and other factors which we are not yet fully aware of. At the same time, religious differences in fertility, about which we now tend to be so much concerned, are likely to diminish. All present studies indicate that church opposition has been able only to moderate, but not to prevent, the use of contraception by its members. If and when contraceptives become cheap and fully effective, and our people become increasingly urbanized, the religious group which has hitherto opposed all contraception will undoubtedly modify its teachings.

No broad generalizations can be drawn at present for other factors. Studies on the relationship between fertility and the health of parents or children are insufficient and contradictory. Downes (1939) reported on the birth rate of couples in Cattaraugus County, New York, when one or both parents were tuberculous. Prior to 1901, at the end of twenty-five years of married life, one hundred women in tuberculous families had an average of 481 children per one hundred women compared with 526 children per one hundred in the general group. But for the period 1900–1929, after sixteen years of married life, one hundred women in the tuberculous group had borne on the average only 261 children as compared to 375 children for the women in the general population. Undoubtedly the use of contraception and improved

health information have had similar results for a number of other diseases having a known hereditary basis.

On the other hand, Reed and Palm (1951) have reported a quite opposite result in a study of a Minnesota family containing the dominant gene for Huntington's chorea. The progenitor of these families came to this country with his brother about the middle of the last century. His brother was not affected. They both had ten children, but since that time, there have been 787 descendants of the infected brother, of whom 716 are living, and only 186 descendants of the sound brother, of whom 167 are living. The authors of the study believe that the gene for Huntington's chorea, in addition to causing the disease, acts directly on the fecundity of the affected person. They compared the number of children ever born to affected persons with the number ever born to their unaffected sibs. The average number of children from affected individuals was $6.07 \pm .09$, and from unaffected sibs, 3.33 ± 0.5. Eight different comparisons from the Dight Institute and from the literature gave similar results. Part or perhaps all of this difference may be accounted for by the fact that those affected with Huntington's chorea undoubtedly bring their families down to a lower social level and thus, at a time when the use of contraceptives varies with social class, tend to a more unrestricted reproduction (cf. Kiser and Whelpton, ed. 1951).

The Indianapolis Study includes a report on fertility in relation to fertility planning and health of wife, husband, and children. The results are inconclusive. Instead of the hypothesized inverse relationship between health and fertility planning, the relationship is direct. However, this direct relation virtually disappears when socio-economic status is held constant. Among couples who planned the number and spacing of their children, there is a substantial increase in fertility rates with rising average rating of health of children both in infancy and after infancy; but small numbers and certain selective factors raise questions as to these findings.

Other studies on the relation of health to fertility are equally inconclusive or contradictory. Anti-toxins and anti-biotics have reduced the effect of natural selection for immunity to many diseases. On the other hand, improved public health facilities, advice on contraceptives, and the segregation and remedial care of many types of sick persons must have considerably reduced their fertility. Certainly this is an important field of study.

In the matter of intelligence, a great many studies have indicated that fertility is inversely related to I.Q. Most of these studies measure the I.Q. of only children or of children in two-child families and compare it to the I.Q. of children in larger families. The small-family children are brighter on the average, and this is true as between families within each socio-economic or occupational group as well as between socio-economic groups. A number of competent students believe that the genetic base for developing intelligence is declining from one generation to another. Other students are less certain or change their minds with every new study.

There are few, if any, studies on the relation of fertility to various traits of personality in human beings, though studies made on animals, particu-

larly dogs, indicate the important part played by genetic factors in accounting for differences in personality. The Indianapolis Study attempted to find the relationship, if any, between general planning and fertility rates, and the relationship of marital adjustment to fertility rates. The trait of general planning might be considered related to aspects of the personality, and it is therefore disappointing that the evidence concerning its relation to fertility was inconclusive (Kiser and Whelpton, 1951).

With respect to marital adjustment, the data for the sample as a whole indicated a decline in marital adjustment with increasing family size. This is partially explained by the fact that marital adjustment declined with decreasing success in preventing unwanted pregnancies. In other words, marital adjustment was found to be positively associated with success in fertility planning. Furthermore, among the number-and-spacing-planned families, marital adjustment was found to increase slightly with fertility and with success in having *as many* children as were wanted.

These rather rambling observations on our present knowledge or lack of it seem to lead us to some inevitable conclusions which, while they are of a negative sort, may stimulate our thinking and are therefore worth putting down. These conclusions are as follows:

First: Until geneticists and psychologists are able to relate a larger number than at present of some objective measurable traits of man to particular aspects of his genetic constitution, especially those which have to do with intelligence and traits of personality, we won't know the direction of human evolution; one man's guess will be as good as another's.

Second: In the United States, or any other country populated by people of Western European descent, the use of contraception has probably invalidated for all but certain genes for defect, one of the basic assumptions of the Hardy-Weinberg Law, namely, that the carriers of a gene reproduce at rates no different from the carriers of an allele of this gene.

Unless it is demonstrated that all genetic stocks are influenced in the same way by the psychological factors which affect fertility, population genetics regarding intelligence and personality in human beings will have to be written, not in the light of Hardy-Weinberg but in terms of the effect of psychological factors.

Third: Until we are able to measure individuals for their genetic characteristics, we cannot have scientifically based specifically genetic programs for the general run of the population. We can, however, have genetic programs for those limited groups in the population whose genetic characters can be determined by some objective means. These are mostly defects, and therefore in the field of public health.

Without waiting for the final advances of the science of genetics, we can also have a sound and acceptable and wholly voluntary program of eugenics for raising the average intelligence and approved personality traits of the population at large, using the science of psychology to de-

termine the factors which affect fertility, and basing the program on mass selection and the progeny test, means which have been eminently successful in improving the strains of domestic animals and plants; but that is another story not appropriate to this paper.

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OPARIN'S HYPOTHESIS AND THE EVOLUTION OF NUCLEOPROTEINS

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With the translation of Oparin's book "The Origin of Life" into English in 1938, there appeared in this country an extensively developed and well-reasoned hypothesis accounting for the origin of life. The major, and immediately appreciated contribution of Oparin was the demonstration that there could have been a great variety of organic compounds before there were living things, as a result of the fact that carbon was first present, not in the oxidized, but in the reduced form. Although this idea was not original with Oparin, his work is mainly responsible for its general acceptance.

Less widely accepted is his account of the mode of transition from a non-living mixture of organic compounds to primary living things. Oparin believed that whole systems of colloidal particles (coacervate droplets) were the first self-reproducing biological units, and that the first organisms were superficially cell-like, rather than gene-like. In the United States, a different school of thought seems to be dominant, one which holds that self-duplicating nucleoprotein molecules or particles either preceded life, or actually were the first forms of life.

Oparin's hypothesis concerning the origin of living from non-living matter supposes the process to have taken place in the following steps:

1. Interaction of compounds such as iron carbide, metallic nitrides, and water early in earth history, which initiated a long period of purely chemical evolution, resulting in the production of a multitude of organic compounds of varying degrees of complexity.

2. Formation of particles of colloidal size, including primary proteins, by polymerization of simpler organic compounds.

3. Organization of colloidal particles into coacervate droplets, which are delimited from the environment by a membrane.

4. Persistence and multiplication of coacervate droplets which possess the ability to assimilate organic compounds from the environment and the ability to divide after growth, leading to the appearance of living systems.

Some corollary theses of Oparin are as follows:

1. As the first living things appeared and biological evolution began, the energy-rich organic compounds of the primeval environment were depleted, so that few compounds from which energy could be extracted by anaerobic metabolism remained.

2. Under these conditions, as a result of natural selection, photosynthetic organisms were evolved from the relatively complex living systems already in existence.

3. With the appearance of photosynthesis, conditions of life altered in a revolutionary way, with production of an atmosphere rich in oxygen, and a relatively inexhaustible supply of food for the non-photosynthetic organisms.

4. With the appearance of an environment rich in free oxygen, aerobic metabolism appeared, and was superimposed upon the older anaerobic metabolic system.

It is probable that Oparin's contribution to the vast amount of organization of biochemistry that has taken place in the last two decades will turn out to have been a major one; in addition, his book provides an exceptionally fine model of the application of the historical (in the sense of evolutionary) approach to basic biological problems, in contrast to what has often been a purely mechanical approach.

Other powerful organizing influences in biochemistry are concerned with the discovery of the biological role of nucleotides, and of their polymeres, the nucleic acids. For example, the discovery of the transferable high-energy phosphate bond, carried on a nucleotide (ATP) contributed to an understanding of the apparent vagaries of the glycolytic cycle, on the one hand, and on the other, of the means whereby synthetic activities could be carried out. Further, there is the fact that desoxyribonucleic acid is regularly connected with genetic phenomena, and the supposition that ribonucleic acid is probably connected with cytoplasmic synthesis of proteins (and, therefore, of enzymes). And, again, virus particles regularly contain nucleoprotein.

Since virus particles and the genes (and, possibly, the RNA-containing particulates of the cytoplasm) were the only demonstrably autoreproductive particles in biological material, the conclusion was reached that the autocatalytic molecules supposed to have preceded or marked the origin of life were not only like viruses and genes in being autocatalytic, but also were probably like them in consisting of nucleoproteins.

As stated by Muller (1947:2) "...all other material in the organism is ...subsidiary to the genetic material, and the origin of life is identified with the origin of this material by chance chemical combination." Another statement of the "molecular," if not nucleoprotein, theory is provided by Beadle (1949:240): "Somehow...there presumably arose molecules with the property of duplicating themselves, that is, capable of catalyzing the process by which they were formed. If such molecules were at the same time sufficiently large and appropriately built to multiply their kind systematically, they could become the ancestors of further lines of evolution, now definitely organic." The same general views are reiterated in the recent book, "Time's Arrow and Evolution," by H. F. Blum, although he regards the question as to whether or not the primitive autocatalytic molecules should be regarded as living as an open one.

Oparin's hypothesis, on the other hand, implies that relatively large, cell-like systems (coacervates) were the first self-reproducing structures, and that growth and division of whole systems represents primary biological growth and reproduction. The coacervate theory of Oparin presents a series

of gradual steps leading up to the origin of living systems. This is not true of the virus or "free gene" theories. As Beadle states (1949:240): "The step by which the first self-duplicating mutable molecule originated is clearly the most difficult one to imagine in the whole evolutionary process." Blum's solution of the problem, is, basically, to assume that the phosphate energy transfer mechanism characteristic of contemporary cells was present in at least rudimentary form in the non-living, chemical environment of the first "free genes." It is the present writer's belief that the high-energy phosphate bond should be regarded as having been evolved in living systems, and therefore to be a result of organic, not of chemical evolution.

Oparin's theory assumes that, before the appearance of coacervates, there must have been particles of colloidal size, which were presumably polypeptides, evolving as a result of purely physicochemical processes. His hypothesis does not require that these be autocatalytic. Polypeptide particles could not have arisen, in the chemical phase of evolution before the origin of life, from spontaneous polymerization of ordinary amino acids, because of the energy relationships involved. Approximately 3,000 calories are required to form the peptide linkage, which is too great an energy differential for polypeptides to be built up from amino acids by spontaneous polymerization. Therefore, polypeptides must have been formed, both before the origin of life, and early in biological evolution, by the polymerization of amino acid-like compounds of higher energy content than that of true amino acids. If this be so, then the depletion of energy-rich compounds in the environment of the first organisms must have reached a critical stage before the low level was reached at which photosynthesis became necessary. This would be a level at which there was a scarcity of precursors at an energy level high enough to polymerize into polypeptides exothermically. However, the complexity of living systems, by this time, could have reached a point where the problem could be solved by evolutionary processes. It could be expected that a depletion of energy-rich protein precursors would take place before a depletion of other energy-rich organic compounds. What is required is that energy from such organic compounds, released by anaerobic metabolism, be concentrated into transferable, energy-rich chemical bonds which can be added to the protein precursors so as to raise them to such an energy level that polymerization can proceed. In contemporary organisms, energy-rich phosphate bonds are formed by internal reorganization of molecular structure of various compounds, following dehydrogenation, and these bonds are transferred to a nucleotide, which can then transfer them to a variety of other compounds. There is some evidence that these high-energy phosphate bonds are used to raise the energy level of amino acids, directly or indirectly, to the point where they can be used in protein synthesis.

In a coacervate droplet which grows at the expense of compounds in the environment, and in which organic compounds can be conveniently concentrated, it could be assumed that growth of the constituent polypeptide par-

ticles could take place by simple polymerization of high-energy "amino acids," with increase in number of the particles occurring by more or less random breakage of the chains after they reach a certain length or size. At first, incorporation into the coacervate droplets of compounds other than polypeptide precursors would be related more to the maintenance of the colloidal system in various states of solation or gelation, or various other subsidiary processes, than to the energetics of synthetic reactions. But from the multitude of organic reactions which could be expected to go on in such systems, it would not be unreasonable to assume that there could be selection for reactions between "extraneous" compounds (those not directly involved as polypeptide precursors), and the amino acids themselves, reactions of a kind which would raise the energy level of the amino acids. Any spontaneous reaction, itself exothermic, between an amino acid and some energy-rich compound which would have the effect of raising the energy level of a true amino acid by well over 3,000 calories would be selected for in an environment which had become poor in naturally occurring high energy amino acid-like compounds. A further development would be the elaboration of metabolic pathways whereby high energy bonds could be formed at several points, to be transferred to the amino acids. From primitive beginnings, such a system could evolve into the contemporary high energy phosphate bond mechanism. Such an evolution could occur more easily inside a membrane-enclosed system like a coacervate droplet than in an environment of dispersed solutes and colloidal particles. With increasing organization of such a system, it would become possible to regularize protein synthesis by means of some spatially organized arrangement of the energy transfer mechanism. Although there is little direct evidence for it, it is an attractive idea to think that the nucleotide polymeres of nucleoproteins indeed represent such an arrangement, as Spiegelman and Kamen (1946), and Muller (1947:24) have suggested. At least, it seems likely that there is not enough evidence to exclude definitely the possibility that the nucleotide polymeres associated with protein synthetic centers are either high energy phosphate donors, or hydrogen acceptors, or both. It seems difficult otherwise to account for the presence of nucleic acid in nucleoproteins, in terms of function, unless they function only as "spacers" in providing the correct configuration for the deposition of polyphosphate nucleotide-amino acid combinations.

Oparin emphasizes the difference in ability to accelerate chemical reactions between relatively non-specific and slow-acting non-biological catalysts and the specific, rapidly acting enzymes which are characteristic of biological reactions. It could be expected that the polypeptide (primary protein) particles of coacervate droplets would exhibit accelerating properties at the non-biological level of catalytic activity, due probably to surface properties of colloidal particles in general, and that along with the evolution of coacervate droplets into living structures, and during the early evolution of living structures, there would be an evolution from the catalytic level of activity of relatively non-specific polypeptides toward the enzy-

matic level of activity of true proteins. This would involve increasing specificity of structure, which would be facilitated by a more or less spatially organized proteo-synthetic energy transfer mechanism. The evolution of a multitude of specific enzymes would, of course, enormously widen the range of organic compounds which could be utilized by living systems either as energy sources or as precursors for protein synthesis, and, more important, make possible increasing precision in biochemical processes.

From the standpoint of energetics, it is possible to visualize the gradual appearance, from more primitive organisms, of complex living things having a high-energy phosphate bond synthetic mechanism, or its equivalent, based on the anaerobic breakdown of organic compounds. Such relatively advanced biological systems could serve as the point of departure for the evolution of photosynthetic organisms by the incorporation of photochemically energized pigments into an already existing energy-generating and transfer mechanism. Although it does not necessarily prove that the above sequence is actually the correct one, it is apparently a fact that contemporary photosynthetic organisms have phosphate bond energy transfer systems.

The views outlined above suggest that nucleoprotein centers, either self-duplicating, or proteo-synthetic, or both, are derived, secondary structures, and that their reproduction is only ancillary to basic biological growth, which is growth and division of the cell. With respect to the evolutionary origin of viruses, these views would imply that animal viruses and bacteriophages are not representatives of the most primitive microorganisms, but are, instead, either parasitic microorganisms which have lost most cytoplasmic functions, or are infectious fragments of the nuclear apparatus of cells, or are a mixture of both. These views would lead to the following summary of the major phases of the origin and early evolution of life:

1. An environment rich in a great variety of organic compounds, produced by chemical evolution.

2. Appearance of particles of colloidal size, including primary proteins, by polymerization of precursors of higher energy levels than contemporary amino acids.

3. Organization of colloidal particles into colloidal systems: coacervate droplets.

4. Evolution of coacervate droplets into the first living things, by attainment of relative stability combined with growth and ability to divide. Increase in number of constituent polypeptide particles by more or less random breakage of growing polymeres.

5. Selection of biochemical systems which would transfer energy to the protein synthetic system, and which would solve the problem presented by a depletion of energy-rich protein precursors in the environment. Gradual emergence of a phosphate bond energy transfer mechanism, and of one of its possible consequences, specific, spatially organized nucleotide polymeres.

6. Accelerated evolution of polypeptides from the non-biological-catalytic to the enzymatic level of activity, based on the regularized production of specific proteins having the necessary specific structures.

7. Division of labor within the nucleic acid proteosynthetic mechanism, so that one component (desoxyribonucleic acid) remains relatively stable from one cell division to the next, preserving certain configurations, with another more labile component (ribonucleic acid) engaging actively in protein synthesis.

8. Appearance of photosynthetic organisms, as a selectional response to depletion of energy-rich compounds in the environment.

9. Appearance of aerobic metabolism. Continued improvement of the spatial organization of the cell, resulting in desoxyribonucleic acid polymeres being organized into chromosomes, ribonucleic acid polymeres into microsomes, differentiation of nucleus and cytoplasm, and differentiation of such cytoplasmic structures as mitochondria, etc.

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THE TRANSFER OF DESOXYRIBOSE NUCLEIC ACID FROM THE TAPETUM TO THE MICROSPOROCYTES AT THE ONSET OF MEIOSIS[1]

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Extranuclear chromatin-like bodies in association with the nuclei and cells of the sporogenous tissue have been noted in numerous species of plants. They have usually been considered to be surplus chromatin which has been extruded from the nuclei of the sporocytes at the synaptic phase of meiosis. Cytochemical analyses have shown that these bodies contain an appreciable amount of desoxyribose nucleic acid.

The nature and function of such chromatin-like bodies have been the objects of considerable conjecture. Diverse interpretations have been advanced such as (1) they cause abnormal divisions of the spore mother cells (Gregory, 1905); (2) they are waste materials (West and Lechmere, 1915); (3) they either serve as a site for protein synthesis or they may become converted into ribose nucleic acid in the cytoplasm of the sporocyte (Sparrow and Hammond, 1947) and (4) they are utilized by the nucleus at the onset of meiosis (Darlington and LaCour, 1946).

MATERIALS AND METHODS

Immature buds of *Lilium regale* and *L. Henryi* were collected at varying stages of development. The anthers and ovary were removed from each bud and fixed. A number of fixing agents were used such as Carnoy's solution with and without chloroform, Helly's solution and Nawaschin's fluid. An acetocarmine smear of a portion of an anther from each bud was made at the time of fixation in order to determine the stage of development within the sporogenous tissue. The remaining anthers of those buds wherein a critical stage of development was present were embedded in paraffin, sectioned and stained. Several staining combinations were used such as Delafield's Haematoxylin and safranin, iodine-crystal violet-picric acid, methyl green-pyronin and the Feulgen reaction with and without HCl hydrolysis. Slides prepared for studies of microsporogenesis in a number of other species of plants were also critically examined.

OBSERVATIONS

Lilium regale and *L. Henryi*,—There is a close correlation between the length of the anthers and the stage of development within the microsporangia in these species of lily. The primary sporogenous cells and those of the

[1]Paper No. 478 from the Department of Genetics, College of Agriculture, University of Wisconsin.

tapetum have become differentiated in each locule of young anthers which are 3 mm in length (fig. 2). The cells of the sporogenous tissue contain dense cytoplasm whereas that in the cells of the parietal tissue is highly vacuolate. Growth of the anther continues as a result of active cell division in the sporogenous tissue and in the outer layers of parietal tissue. The cells of the intervening tapetal layer do not, as a rule, undergo further division. An occasional one may divide in an anticlinal plane. The tapetal cells gradually increase in size during the early course of anther development and have more than tripled in volume by the time the cells of the sporogenous tissue are undergoing the last premeiotic divisions which occur in anthers that are 4 to 5 mm in length (fig. 3). They continue to enlarge and their nuclei undergo mitosis giving rise to binucleate cells. The microspore mother cells likewise increase in size and their nuclei have advanced to the leptotene stage of meiosis in anthers in which the tapetal nuclei are in stages of division (fig. 4). They continue to enlarge as meiosis proceeds and the binucleate tapetal cells become somewhat flattened between them and the outer parietal layers of cells.

Globules with chromatin-like staining properties, since they are dyed red with safranin and blue with both crystal violet and methyl green, form at the surface of the tapetal nuclei in anthers ranging from 5 to 6 mm in length. The nuclei are irregular in shape and size during the course of formation of these bodies (figs. 5 and 6) but recover their normal form after becoming rid of them. The globules are Feulgen-positive, which indicates that they are composed of an appreciable amount of desoxyribose nucleic acid (DNA). After becoming detached from the nuclei they move through the cytoplasm toward the inner wall of the cell (figs. 7 and 8) where they collect in abundance and then gradually pass through the cell wall and migrate between the microsporocytes. The globules are more or less uniform in size up to the time they leave the tapetal cells. Bodies of various sizes are present among the microsporocytes in anthers ranging from 7 to 8 mm in length.

The nucleus of the microsporocyte is centrally located within the cell just prior to the onset of meiosis (fig. 4). It gradually shifts its position toward the periphery of the cell and comes to lie in close contact with the cell wall. The somewhat polarized chromosomes are loosely paired during the course of this shift in position of the nucleus (fig. 7 and 8). Pairing is particularly evident in the region of the centromeres. The threads are oriented so that the centromeres are adjacent to that portion of the nuclear membrane which is in close contact with the cell wall.

The Feulgen-positive bodies between the microsporocytes collect opposite those regions where the nuclei are in contact with the cell walls (fig. 8). They become closely pressed to the wall of the microsporocyte and gradually pass through the wall into the adjacent nucleus and become associated with the paired chromosomes bringing them into a close relationship (figs. 9, 10 and 11). The chromosomes increase in diameter and take

a heavier stain coincidental with the ingestion of these chromatin-like materials.

Such an inward movement of the Feulgen-positive substance is clearly evident in the two photomicrographs of the same microsporocyte of *L. Henryi* taken at different foci as shown in figure 1, *a* and *b*. The globules are at the surface of the cell. The chromosomes are larger in diameter and closely paired immediately opposite these materials, indicating that they are being imbibed by the nucleus. The distal ends of the chromosomes are filamentous and loosely paired.

The droplets gradually shrink in size as they are absorbed and at the same time zygotene pairing advances (figs. 10 and 11). Shortly after they

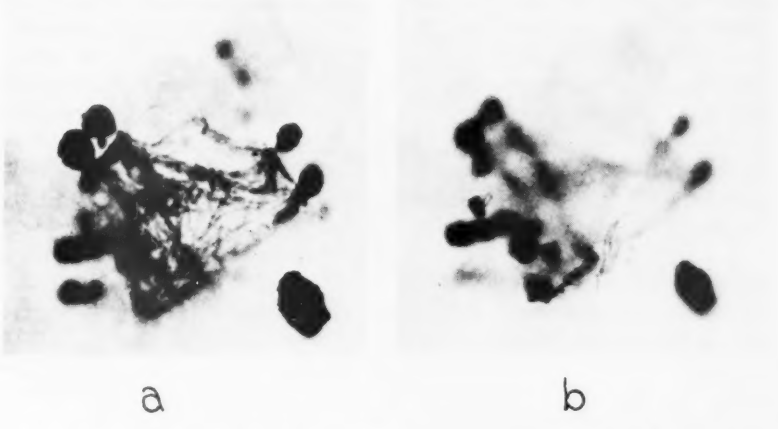
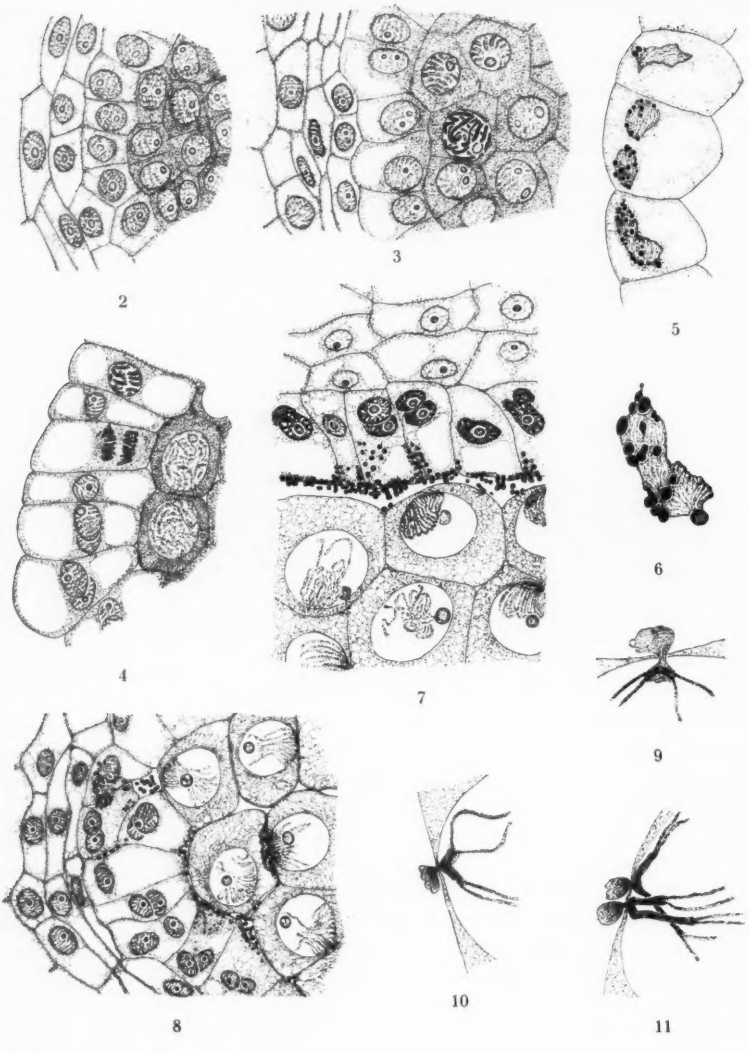


FIGURE 1. Photomicrographs of the same microsporocyte of *Lilium Henryi* taken at two foci, *a* and *b*, showing inward movement of Feulgen-positive materials. (Courtesy of W. Plaut.)

have been ingested the nucleus resumes a more or less central position within the microsporocyte. There is little, if any, evidence of Feulgen-positive substances in the intercellular spaces between the spore mother cells at the later stages of meiosis.

When the methyl green-pyronin staining combination is used, the globules which are formed in the tapetal cells and pass thence into the locule are blue in color similar to that of the chromatin within the nuclei. The nucleoli and cytoplasm of the microsporocytes are stained pink, demonstrating the presence of ribose nucleic acid (RNA). The vacuolate cytoplasm of the tapetal cells is almost colorless, which indicates that little, if any, RNA is present.

The tapetum functions as a nurse tissue for the microsporocytes during the subsequent course of meiosis. When the young spores of a tetrad have become separated from one another the tapetum again assumes a special role. Waxy materials are synthesized therein and are gradually excreted



FIGURES 2 to 7. *Lilium regale.*

FIGURE 2. Transverse section of a portion of a 3 mm anther showing parietal tissue, tapetal cells and sporogenous tissue.

FIGURE 3. T.s. of a 5 mm anther showing late prophase of last premeiotic mitosis.

FIGURE 4. Tapetal nuclei undergoing mitosis in formation of binucleate cells.

FIGURE 5. Tapetal cells with Feulgen-positive bodies forming at surface of nuclei.

FIGURE 6. Nucleus of a tapetal cell with Feulgen-positive bodies on its surface.

FIGURE 7. T.s. of 6 mm anther. Feulgen-positive bodies moving toward microsporangium.

into the locule where they become associated with the wall of the spore during the course of formation of the exine of the developing pollen grain (fig. 12). After the waxy materials have been utilized the tapetal cells collapse and ultimately disintegrate. Little evidence of remnants of the tapetum can be detected in the locules of a mature anther.

Other Species—Bodies with chromatin-like staining properties at the surface of the tapetal nuclei were likewise found to be present in anthers of a number of other species of angiosperms wherein the microsporocytes were in a leptotene-zygotene stage of meiosis. The release of such bodies from the tapetal nuclei, their passage from the tapetum into the intercellular spaces within the sporogenous tissue, their accumulation opposite the peripherally located nuclei of the microsporocytes and ultimately their movement into such nuclei were clearly evident in preparations of *Tradescantia virginiana, Allium cepa, Podophyllum peltatum, Delphinium Ajacis, Menispermum canadense, Bryophyllum pinnatum, Galega officinalis, Scabiosa atropurpurea, S. caucasica, Ambrosia trifida, Heliopsis helianthoides, Gaillardia aristata, Achillea millefolium, Lactuca scariola* and *Crepis capillaris.* A series of stages showing the formation and movement of these bodies in *Lactuca scariola* is depicted in figures 13, 14 and 15. Their movement into the microsporocytes of *Allium cepa* and *Galega officinalis* is shown in figures 16 and 17.

The presence of such bodies between the microspore mother cells and in close association with their peripheral nuclei was noted in preparations of anthers of *Zea mays, Yucca filamentosa, Rhoeo discolor, Medicago sativa, Melilotus alba* and *Phryma leptostachya.* The ingestion of these bodies into the nuclei of microsporocytes of *Yucca filamentosa, Medicago sativa* and *Melilotus alba* is shown in figures 18, 19 and 20 respectively. Undoubtedly the tapetal nuclei would be found to be the source of such bodies if the critical stages of anther development were available for examination and study.

Although some of these globules may appear to lie within the cytoplasm of an adjacent microsporocyte (figs. 8, 15, 16 and 20) they are found to lie on the surface of that cell when the difference in focal planes is taken into consideration. If the spore mother cells are well separated, as in smear preparations, the bodies remain associated with the cell which they are entering and are readily separated from adjacent cells.

Megasporogenesis—A single large megasporocyte is normally present in each ovule of *Zea mays, Euchlaena Mexicana, Lilium regale, L. martagon,*

FIGURES 8 to 11. *L. Henryi.*

FIGURE 8. T.s. of anther showing inward movement of Feulgen-positive bodies from the tapetum and their accumulation adjacent to the peripherally located nuclei of the microsporocytes.

FIGURE 9. Detailed sketch of a single globule entering the nucleus and becoming associated with a pair of chromonemata in the region of the centromere.

FIGURES 10 and 11. Somewhat later stages showing movement of Feulgen-positive material along the pairing chromonemata.

Erythronium americanum and *Melilotus alba.* Two or three such cells occur in the ovules of *Medicago sativa.* The nucleus of the megasporocyte is more or less centrally located within the cell until it reaches the leptotene stage of meiosis. Thereafter it moves to a peripheral position. The pairing chromosomes which are more or less polarized within the nucleus become oriented so that the centromeres lie on that side of the nucleus which is adjacent to the cell wall. The nucleus resumes a central position as it approaches the pachytene stage of meiosis. This movement of the nucleus, which is similar to that found during a comparable early period of meiosis in the microsporocyte, suggests that the adjacent nucellar tissue may be supplying some material that is necessary for the completion of meiosis.

A critical examination was made of developing ovules of *Lilium regale* and *L. martagon* wherein the megasporocytes were in such early stages of meiosis. It was found that globules of chromatin-like material, since they took the usual chromatin stains and were Feulgen-positive, appear at the surface of the nuclei of the surrounding nucellar cells. These globules move toward the megaspore mother cell, pass through the cell walls and collect immediately opposite its peripherally located nucleus. This reserve material appears to be necessary for close chromosome pairing and the completion of meiosis.

DISCUSSION

Extra-nuclear chromatin associated with the synaptic stage of microsporogenesis has been reported as occurring in many species of angiosperms. The usual interpretation following such observations is that this surplus chromatin-like material is moving from the nucleus into the cytoplasm of the same or an adjacent mother cell. Such a phenomenon was first described by Koernicke (1902) as occurring in *Crocus.* He concluded that a portion of the chromatin from a nucleus of one microspore mother cell passes through an opening in the cell wall into the cytoplasm of an adjacent mother cell. Digby (1909) noted chromatin bodies in *Galtonia candicans* which she considered to be budded off from the nuclei prior to synapsis. Such bodies were described as passing from the nucleus into the surrounding cytoplasm, penetrating the cell wall and entering the neighboring cell. If the writer's interpretation of her illustrations is correct the bodies are lying between the microsporocytes at synapsis as shown in her figure 2. They are apparently moving into the peripherally located nuclei at somewhat later stages of meiosis (see her figs. 5, 9, 15 and 16).

Gates (1911) likewise described such a movement of extranuclear chromatin and termed the phenomenon "Cytomixis." Later Gates and Rees (1921) described a similar movement of such materials from the nucleus of one microsporocyte to the cytoplasm of an adjacent mother cell in three species of lettuce (*Lactuca sativa, L. murialis* and *L. scariola*). If such were the case these bodies should be located immediately opposite the nuclei from which they were derived whereas in the material examined in

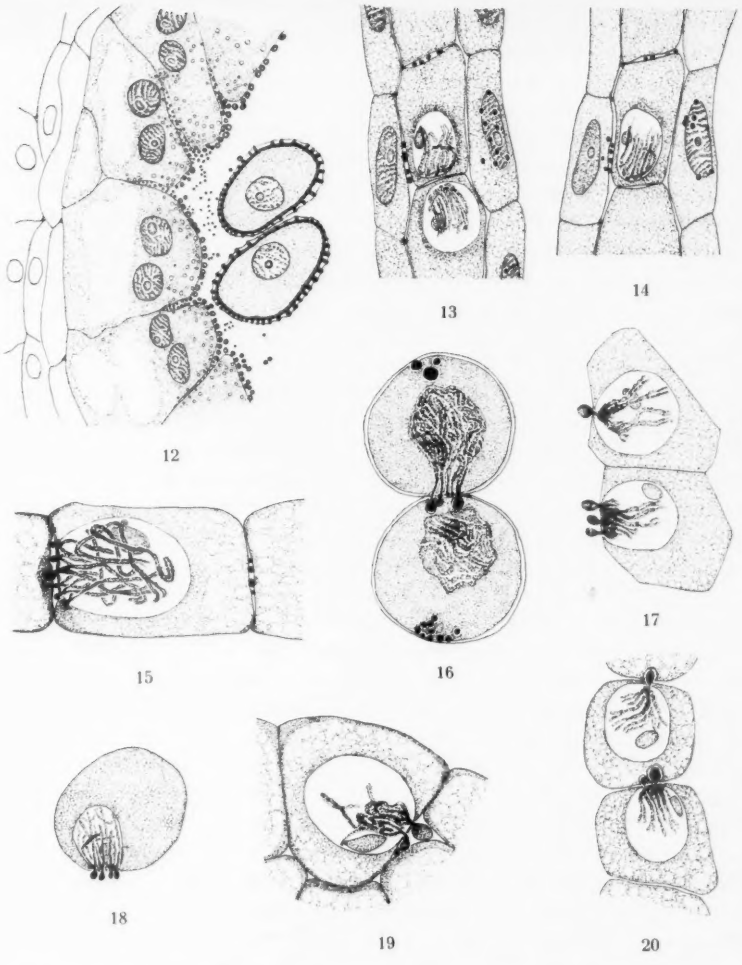


FIGURE 12. T.s. of portion of older anther showing formation of waxy materials within the tapetum and the movement of such materials into the microsporangium.

FIGURES 13 to 15. *Lactuca scariola.*

FIGURES 13, 14. L.s. of portion of theca showing formation of bodies at surface of tapetal nuclei and their inward movement.

FIGURE 15. Microsporocyte. Chromatin-like materials moving into the nucleus and becoming associated with the pairing chromonemata.

FIGURES 16 to 20. Chromatin-like materials at surface of microsporocytes and moving into peripherally located nuclei.

FIGURE 16. *Allium cepa.*

FIGURE 17. *Yucca filamentosa.*

FIGURE 18. *Galega officinalis.*

FIGURE 19. *Medicago sativa.*

FIGURE 20. *Melilotus alba.*

the course of the present investigation they occur on all sides of the spore mother cells. (figs. 13, 14 and 15).

Other investigators (see Gates and Rees, 1921, for references) observed such extrusion of chromatin material. It was thought by some that a nucleus which had lost a portion of its chromatin would not be able to complete normal development. Others considered such extrusion to be a normal condition due to active metabolism at the synaptic phase. Gregory (1905) described it as occurring in *Lathyrus odoratus* and thought he had evidence for an abnormal division of the pollen mother cells by constriction. West and Lechmere (1915) noted the phenomenon in *Lilium candidum* and considered the extruded materials to be waste products.

More recently Sparrow and Hammond (1949) detected such bodies in association with the nuclei at the leptotene-zygotene stage of microsporogenesis in eight species of plants. A positive Feulgen reaction plus a high absorption of ultraviolet light at 2537Å and 2650Å was considered conclusive evidence that these bodies contain desoxyribose nucleic acid. They concluded that the bodies originate in or at the surface of the nucleus of the microsporocyte and migrate into the cytoplasm, and suggested that such bodies may either function as sites of protein synthesis or may become converted into RNA in the cytoplasm. Figures 5 and 8 in their paper may be interpreted as showing this material at the surface of the cells. Although similar bodies were found to be present in the tapetal cells of *Trillium erectum* and *Lilium Henryi* as well as being associated with the microsporocytes, no further study was made of that tissue.

Darlington and LaCour (1946) were the first to suggest that these materials were being utilized by the nucleus at the onset of meiosis. They noted masses of Feulgen-positive materials of fairly uniform size in association with the nuclei of young megaspore mother cells at the opening of prophase in three species of Fritillaria. Such masses were not associated with either the nucleolus or the chromonemata. They gradually shrank in size and ultimately disappeared with the onset of meiosis. These masses were considered to be the source of DNA for the development of the chromosomes. The origin of such "dumps" of nucleic acid was not indicated.

According to Painter (1940) the cytoplasm of both the tapetal cells and the sporogenous tissues in anthers of *Rhoeo discolor* are extremely rich in RNA prior to the onset of meiosis. Since the RNA disappears from the cytoplasm with the initiation of meiosis he concluded that this material passes into the nucleus and is changed into DNA. The tapetal plasmodium is presumed to be the source of the large amounts of RNA which accumulate in the cytoplasm of the pollen grains. Painter did not follow those early stages of meiosis where the nucleus of the microsporocyte assumes a peripheral position.

Swift (1950) determined the quantitative changes of DNA during mitosis in root meristem and during microsporogenesis in three species of Tradescantia. He found that the prophase values were twice the telophase values during somatic mitosis in the actively meristematic tissues

of the root tips and in premeiotic sporogenous tissues. The amount of DNA doubled between the leptotene and zygotene stages of meiosis. This would suggest either an active synthesis of DNA during that short interval or an outside source of this material. Swift found that the nucleus of each spore immediately after the second maturation division possessed half the amount of DNA which was present at leptotene.

Swift's findings are at variance with those of Serra (1947), who noted a relative lack of nucleoproteins at the onset of meiosis. Serra considered that this lack is probably the consequence of a too rapid rate of somatic multiplication of the sporogenous cells. Coincidentally the cytoplasm increases and the whole cell, as well as its nucleus, is markedly larger when meiosis is initiated. As a result there is not a sufficient supply of nucleoproteins for such an intense growth and at the same time an adequate amount available to the chromosomes. Meiotic pairing thus appeared to Serra to be a consequence of a slower deposition of nucleoproteins on the chromonemata during prophase when compared to a similar stage in mitosis where the chromosomes are heavily charged with nucleoproteins from the beginning. He came to the conclusion that the distribution and balance of nucleoproteins between the cytoplasm and the nucleus are the principal agents of meiotic pairing.

Earlier, Gregory (1940) had excised anthers of *Lilium longiflorum* and placed them in a nutrient solution. Such anthers behaved differently, depending on the length of the anther and the stage of development within the sporangia at the time of excision. Active mitosis continued in the sporogenous tissue for 12 days in anthers excised at 3 mm in length, and then gradually ceased. Toward the end of the mitotic period the cells lost their characteristic appearance, becoming vacuolated and elongated, and were similar in size and shape to those of the parietal tissues. The last mitoses prior to meiosis were present in anthers which were 5 mm long at the time of excision. Such sporogenous cells differentiated into microspore mother cells and then disintegrated. Meiosis continued through both divisions but the spores degenerated in anthers which were excised when the microsporocytes were at diplotene. Gregory concluded therefrom that failure of meiosis to occur in anthers excised prior to diplotene and the failure of pollen formation in anthers excised at diplotene is not due to a lack of nutrients but that some accessory substances are transported into the anthers which are necessary for the normal sequence of events.

The buds on the growing plants of *L. regale* and *L. Henryi* develop to such an extent that the enclosed anthers have grown from 3 to 6 mm in length within the course of two to three days. During this short interval the premeiotic mitoses are completed and the microsporocytes have reached the leptotene stage of meiosis. Since Gregory found that active mitosis would continue in the sporogenous tissue for three to four times the typical length of time in excised 3 mm anthers which were placed in a nutrient solution, it would appear that there is no lack of nucleoproteins for chromosome formation as a result of such activity as hypothecated by Serra.

It is evident in the light of the present findings that the onset of meiosis is not accomplished by the microsporocytes alone but is brought about as the result of an interaction between these cells and the adjacent tapetal tissue. Accessory substances which are necessary for meiosis are made available to the microsporocytes by way of the tapetum at an optimum stage of development.

An analogous phenomenon occurs during the course of development of the primary oöcyte in certain insects. According to Schrader (1951) the somatic cells in the end chambers of the ovary break down and contribute to the nutritive materials for the developing oöcyte. An irregular fusion of nuclei is involved in the breakdown process. Droplets of DNA are extruded through the membranes of nuclei located in a particular region of the end chamber and join the stream of cytoplasmic materials which enters the developing oöcyte. Since the DNA apparently undergoes certain changes and becomes Feulgen negative Schrader concludes that a depolymerization occurs. Inasmuch as meiosis does not occur until late in the development of the oöcyte it may possibly be that some of the surplus DNA is utilized by the nucleus at the onset of the maturation divisions.

Little attention has been given to the role of the tapetum during pollen formation. Kosmath (1927) examined the tapetum of a number of angiosperms during that interval. He discovered that the inner walls of the tapetal cells in many instances showed the same behavior to reagents and stains as did the exine of the pollen which suggested that the walls are either cutinized or posses cutin-like substances. Such cutinization occurs concurrently with the formation of the exine of the pollen. He assumed the presence of such cutin-like cell membranes to be associated with a secretory tapetum. Later Gorczynski (1934) observed the initiation of the development of the exine of the pollen of Cardamine to be on that surface of the grain which faces the tapetum (cited from Maheshwari, 1950). This would indicate the tapetum as being the source of the waxy materials which are necessary for the formation of the exine.

SUMMARY

The tapetum of the anther secretes specific substances at definite stages of development of the enclosed sporogenous tissue, as well as nutrients for its growth and differentiation. Globules with chromatin-like staining properties form at the surface of the tapetal nuclei when the enclosed sporogenous cells are in a late leptotene stage of meiosis. They are Feulgen-positive, indicating that they contain an appreciable amount of desoxyribose nucleic acid. The globules move from the nuclei to the inner faces of the cells, pass through the cell walls and migrate between the microspore mother cells. The nuclei of the microsporocytes move from a central position to a peripheral one. During the course of this shift in position the loosely paired and somewhat polarized chromosomes become oriented so that the centromeres are adjacent to that portion of the nuclear membrane which is in close contact with the cell wall. The chromatin-like

bodies between the microsporocytes collect opposite the regions where the nuclear membranes and cell walls are in contact. Their contents move through the walls into the adjacent nuclei and become associated with the paired chromosomes, bringing them into a close relationship. The formation of such bodies in the tapetum, their movement into the locule and ultimately into the nuclei of the microsporocytes has been observed in 17 species of angiosperms. The presence of such bodies between the spore mother cells and in close association with their peripherally located nuclei was noted in an additional six species. Chromatin-like materials likewise move from the nucellar cells of the ovule to the megasporocyte at the onset of megasporogenesis in *Lilium regale* and *L. martagon*.

Droplets of a waxy material are later synthesized in the cytoplasm of the tapetal cells. These are secreted into the locule where they contribute to the formation of the exine of the developing pollen grains.

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AN EXAMPLE OF THE INFLUENCE OF MODIFYING GENES IN NEUROSPORA*

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The influence of genetic modifiers, those genes which affect the expression of other genes, has been demonstrated in a wide variety of organisms. In *Neurospora crassa* the influence of modifiers is suggested by quantitative differences in growth substance utilization among different reisolates of a mutant strain (Good, Heilbronner, and Mitchell, 1950), and genetic suppression (Houlahan and Mitchell, 1947) may be regarded as an extreme type of modification. In addition, Houlahan and Mitchell (1948) and Mitchell and Mitchell (1952) have demonstrated extensive interactions among genes causing pyrimidine, lysine, and arginine requirements, and Srb (private communication) has found a case in which a single gene modifier appears to control the ability of a proline- or ornithine-utilizing strain of Neurospora to utilize arginine or citrulline. The data to be presented here deal with an instance in which the modification is such that different reisolates of a tryptophane- or nicotinic acid-utilizing mutant appear to be blocked at different steps in the pathway by which Neurospora synthesizes tryptophane and nicotinic acid. For some of the details of this pathway the reader is referred to the recent reviews of Mitchell (1950) and Horowitz and Mitchell (1951). Miss Dorothy Newmeyer, of Stanford University, who has used some of the strains which were used in this work, has also encountered some of the phenomena reported here.

EXPERIMENTAL

Mutant strains

Three types of mutants, differing in their abilities to utilize certain growth substances, were used in the crosses to be described here. For convenience these types have been designated 1, 2, and 3. The isolation number of the type 1 strains which were used in the crosses is C86 and that of the type 3 strains is 39401. Mutants C86 and 39401 have been described in the literature (Gordon, Haskins, and Mitchell, 1950). The origin of the type 2 strains which were used in the crosses will be described later in this report.

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[1] Atomic Energy Commission Predoctoral Fellow.

All three of the mutant types utilize indole, tryptophane, kynurenine, 3-hydroxykynurenine, 3-hydroxyanthranilic acid, nicotinic acid, and nicotinamide. In addition, strains of type 2 utilize anthranilic acid, and strains of type 1 utilize anthranilic acid, phenylalanine, tyrosine, and quinic acid. Table 1 lists quantitative responses of the three types to minimal medium, phenylalanine, anthranilic acid, tryptophane, and nicotinamide.

Crosses of the mutant types to wild type

Asci were dissected from crosses of the three mutant types to wild type, and strains derived from each of the four spore pairs of each ascus were cultured on nicotinamide slants and then tested in 3 inch tubes of minimal

TABLE 1

FOUR-DAY DRY WEIGHTS PRODUCED BY MUTANT TYPES 1, 2, AND 3. GROWTH TESTS WERE CARRIED OUT AT 25° C. USING 125-ml. ERLENMEYER FLASKS CONTAINING 20 ml. OF LIQUID MEDIUM.*

Mutant type	No. of ascospore cultures tested	Four-day dry weights (mg.) produced on								
		Minimal	DL-Phenylalanine 500 γ		Anthranilic acid 200 γ		L-Tryptophane 500 γ		Nicotinamide 20 γ	
			Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
1	177	trace	42.6	0.6	64.9	0.6	76.3	0.8	76.7	0.5
2	107	"	9.5	0.9	55.1	0.9	71.8	1.2	69.4	0.8
3	243	"	trace		1.1	0.2	49.0	0.6	70.9	0.5

*The minimal medium described by Beadle and Tatum (1945) was used in all the experiments described here.

medium and minimal plus nicotinamide. Those strains which appeared to be mutant were then further tested in 125-ml. Erlenmeyer flasks, as described in Table 1, and were classified as type 1, 2, or 3 (Table 2). Classification on this basis was relatively easy and straightforward except in the case of the cross of strain 3A × wild type Em 8815-3a. The progeny of this cross included a number of ascospore cultures which were borderline cases, and were therefore somewhat difficult to classify.

At the beginning of the investigation of these crosses and also of the intercrosses among mutant types (next section) both members of each mutant spore pair were tested. A total of 123 mutant pairs were tested in this way, and it was found that the agreement in growth response between the two members of any pair was excellent. Thereafter, ascospores were dissected out and tested in pairs rather than individually.

From table 2 it may be seen that each ascus from the crosses of the mutant types to wild type contains two wild-type spore pairs. Testing on the four growth substances in addition to minimal medium permits subdivision of the mutant offspring into types 1, 2, and 3; and it is found that all three types are recovered from the 3A × wild type crosses, while 1A × wild type and 2A × wild type both yield mutant types 1 and 2. This re-

TABLE 2

CLASSIFICATION OF ASCI FROM CROSSES OF MUTANT TYPES 1, 2, AND 3 TO WILD TYPE. (STRAINS 8a, 25a, AND Em 8815-3a ARE WILD TYPES.)

Cross	No. of asci tested	Constitution of asci: Number of spore pairs of the indicated types.			
		Wild	1	2	3
1A × 8a	18	2	2	0	0
	3	2	0	2	0
	1	2	1	1	0
	22				
2A × 8a	4	2	1	1	0
	1	2	2	0	0
	5	2	0	2	0
	10				
3A × 8a	4	2	0	0	2
	8	2	0	1	1
	2	2	1	0	1
	14				
3A × 25a	10	2	0	0	2
	1	2	0	1	1
	2	2	1	0	1
	13				
3A × Em 8815-3a	6	2	0	0	2
	1	2	0	2	0
	1	2	1	1	0
	1	2	2	0	0
	5	2	1	0	1
	14				

covery of mutant offspring which are nutritionally different from the mutant parent suggests that genetic modifiers are influencing the phenotype of the mutant offspring. This suggestion is supported by the observation that in a total of 24 instances, two of the mutant types are found in a single ascus.

Intercrosses among mutant types

In further studies of the three mutant types, intercrosses were analyzed with the results shown in table 3. The 2A strain which was used in these crosses was derived from one of the type 3 × 1a crosses referred to below, and strain 2a came from the cross of 3R (anthran.) to wild type 8a. The origin of 3R (anthran.) is described in the next section. It will be seen from table 3 that crosses 2A × 2a and 3A × 2a gave rise to a new mutant phenotype, type 4. Type 4 strains are able to utilize kynurenine, 3-hydroxykynurenine, 3-hydroxyanthranilic acid, nicotinic acid, and nicotinamide, but, unlike the other types, they grow very poorly on indole and tryptophane. The average 4-day dry weights produced by 39 different type

TABLE 3

CLASSIFICATION OF ASCI FROM INTERCROSSES AMONG MUTANT TYPES 1, 2, AND 3

Cross	No. of asci tested	Constitution of asci: Number of spore pairs of the indicated mutant types			
		1	2	3	4
1a × 1A	11	4	0	0	0
	3	2	2	0	0
	14				
1a × 2A	5	2	2	0	0
	4	3	1	0	0
	1	1	3	0	0
	1	4	0	0	0
	11				
1a × 3A	7	1	1	2	0
	3	2	0	2	0
	1	0	2	2	0
	11				
2a × 2A	1	1	0	2	1
	2	2	0	0	2
	1	0	1	2	1
	2	1	1	1	1
	3	1	2	1	0
	2	1	2	0	1
	1	0	2	0	2
	3	0	1	3	0
	1	2	0	1	1
	2	0	2	1	1
	18				
2a × 3A	3	0	1	2	1
	10	0	0	2	2
	1	0	2	2	0
	1	0	0	3	1
	15				
3a × 3A	19	0	0	4	0

4 strains on 500γ of L-tryptophane and on 20γ of nicotinamide were 6.3 ± 1.2 mg. and 72.9 ± 1.3 mg., respectively.

It is noteworthy that all of the ascospores from the dissected asci gave rise to mutant strains. In addition, approximately 15,000 random ascospores from crosses of two different type 3 strains to strain 1a were plated on minimal agar using an adaptation of the method described by Lein, Mitchell, and Houlahan (1948). Approximately 97 per cent of the spores germinated and no wild types were found. Thus it appears that the mutations which prevent the growth of the various types on minimal medium are either allelic or else very closely linked. In agreement with this conclusion is

the fact that attempts to form phenotypically wild heterocaryons among the four mutant types have been unsuccessful.

Adaptation of a type 3 strain to anthranilic acid

As shown in table 1, strains of type 3 do not ordinarily utilize anthranilic acid. It was found, however, that a certain reisolate of this type, designated 3R, which had been maintained in the stocks for a period of several years occasionally would start growth after two or three days of incubation in liquid culture on anthranilic acid. This reisolate was cultured on slants of minimal agar supplemented with 5γ of anthranilic acid/ml. and although it was somewhat slow to start on this medium, the strain eventually produced abundant growth. The response of this culture to phenylalanine, anthranilic acid, tryptophane, and nicotinamide in liquid medium appeared to be unchanged after a single transfer to anthranilic acid agar. Transfers to anthranilic acid slants were continued, however, and after the seventh consecutive transfer the strain was again tested, this time on quinic acid, tyrosine, phenylalanine, anthranilic acid, indole, tryptophane, and nicotinamide. All of these substances were utilized, and it was found that, within limits, increasing the concentration of any of them produced increased growth of the mold. Having acquired the ability to utilize all these compounds, 3R now resembled a type 1 strain. This adapted strain will be referred to as 3R(anthran.). Mutant progeny from a cross of 3R(anthran.) to wild type 8a were found to be predominantly of type 3, while those from the cross of strain 1A to wild type 8a (Table 2) included no type 3 strains. Thus it is apparent that 3R(anthran.) differs genetically from strain 1A although it is nutritionally similar to the type 1 strains.

A genetic suppressor

In the course of attempting a further genetic analysis of 3R(anthran.) this adapted strain was crossed with mutant strain 1a, and approximately 4000 ascospores were plated on minimal agar. Germination of the plated ascospores was approximately 98 per cent and on the basis of hyphal length, approximately 5 per cent appeared to be wild type. Five of these spores were transferred to agar slants, and testing of the resulting cultures showed them indeed to be phenotypically wild. In an effort to learn whether this behavior might be the result of genetic suppression, the five ascospore cultures were crossed to wild types 7A or 8a. Mutant spores were found among the progeny of each cross, indicating that genetic suppression had occurred. A similar case has been described by Houlahan and Mitchell (1947).

Asci were then dissected, a suppressor-carrying wild-type strain and two suppressed-mutant strains were selected, and crosses were made as shown in table 4. The action of the suppressor was tested on strains 10575 and E5029 as well as on strains of types 1, 2, and 3. Strain 10575 requires either indole or tryptophane for growth, and strain E5029 requires 3-hydroxykynurenine, 3-hydroxyanthranilic acid, nicotinic acid, or nico-

TABLE 4

CROSSES INVOLVING THE SUPPRESSOR (S); SUPPRESSED MUTANT (SM); MUTANT STRAINS 1a, 2a, 3a, 10575, AND E5029; AND WILD TYPES 8a AND 7A.

Cross	No. of asci tested	No. of asci with the indicated ratio of wild-to mutant-spore pairs		
		4:0	3:1	2:2
S × 8a	15	15	0	0
S × SM-a	14	14	0	0
S × 1a	17	2	7	8
S × 2a	13	0	3	10
S × 3a	15	0	5	10
SM-a × 7A	14	2	12	0
SM-A × 8a	12	2	8	2
SM-A × 1a	16	0	0	16
S × 10575	22	0	0	22
S × E5029	24	0	0	24

tinamide (Mitchell, 1950). The analysis of asci shown in table 4 was based mainly on tests using 3-inch tubes of minimal medium and minimal plus nicotinamide (2.5 γ/ml.), although some of the cultures were tested in flasks. Progeny of the cross S (suppressor) × 10575 were tested in tubes of minimal medium and minimal plus L-tryptophane (50 γ/ml.). In these crosses the suppressor exhibits the behavior of a single gene whose action repairs in some way the function of the mutant gene which types 1, 2, and 3 have in common, *i.e.*, the mutation which distinguishes these strains from wild type, but whose action is ineffective in repairing the functions which strains 10575 and E5029 have lost by mutation.

The influence of the suppressed mutant nuclei which are evidently present in the 3R (anthran.) culture is not certainly known. It seems possible that the presence of a few such nuclei changes the phenotype of the strain from type 3 to type 1, but an attempt to create a type 1-like culture by artificially mixing suppressed-mutant conidia with type 3 conidia failed. In this attempt, several groups of flasks containing minimal medium or minimal supplemented with phenylalanine, anthranilic acid, tryptophane, or nicotinamide were inoculated with a conidial suspension from a type 3 strain, and simultaneously with a dilution series of suppressed-mutant conidia. It was found that those groups receiving a relatively concentrated inoculum of the suppressed-mutant conidia were phenotypically wild, while those with a dilute inoculum were like type 3.

DISCUSSION

Restated very briefly, the principal experimental facts are these:

(1) Crosses of types 1, 2, and 3 to wild type produce asci each of which has two mutant and two wild-type spore pairs, but the mutant offspring differ, in many cases, from the mutant parent, and in numerous asci the two mutant spore pairs differ from each other.

(2) Intercrosses among the three types produce no wild-type progeny, but many of the asci have three or four phenotypically different kinds of spore pairs.

(3) A culture which is nutritionally like the type 1 strains has been obtained from a type 3 strain by taking the latter strain through repeated transfers to anthranilic acid agar slants. Approximately 5 per cent of the progeny from a cross of this type 1-like culture to strain 1a were phenotypically wild, but subsequent testing showed that they were actually suppressed mutants.

It is by no means certain that the alteration in phenotype of the type 3 strain referred to in the third observation listed above is a result of the heterocaryosis which evidently exists in the 3R (anthran.) culture. If the assumption is made, however, that heterocaryosis is the cause, then one might ask if the seemingly odd progeny from the various crosses listed in tables 2 and 3 might not be due to the presence, in varying proportions, of suppressed-mutant nuclei in the ascospore cultures. The inadequacy of this interpretation is indicated by several experimental facts. First, several transfers to anthranilic acid agar were required before the type 3 strain assumed the nutritional characteristics of a type 1 strain. The need for conditions which favored the selection of certain types of nuclei is indicated. The ascospore cultures listed in tables 2 and 3, on the other hand, displayed their characteristic phenotypes after they had been transferred directly from the minimal agar plates on which they were allowed to germinate, to slants of nicotinamide agar.

Secondly, there is no evidence that ordinary type 1 or type 3 cultures contain any wild-type or suppressed-mutant nuclei, for in 15,000 ascospores plated from two different crosses between the two types, no wild-type offspring were found. Wild types were similarly absent from the dissected asci from intercrosses among types 1, 2, and 3.

A third point against the heterocaryosis hypothesis is found in the similarity which exists between the two members of any spore pair. It has been mentioned that the growth responses of the two members of any spore pair were found to be essentially identical. If these responses were dependent on spontaneous suppressor mutations and the heterocaryosis resulting from these mutations, good agreement within spore pairs would not be expected. If the growth responses were a reflection of genetic constitution, on the other hand, one would expect to find good agreement within pairs.

Finally, if heterocaryosis were responsible for the phenotypes, it seems unlikely that it would be possible to get a strain which would breed true. It was found, however, that in the 3a × 3A cross listed in table 3 all offspring were of type 3. The 3a parent in this case came from a cross of 3A × wild type 8a.

Attempting to account for the experimental observations by assuming an allelic series in which the different alleles lead to altered nutritional requirements is similarly unsatisfactory, for if two strains carrying allelic mutations were crossed, one would expect to recover only two phenotypes (those of the parental strains) from each ascus. In the present case, many of the asci listed in tables 2 and 3 contain representatives of three different types, and two asci have spores of four different types.

It appears, then, that types 1, 2, 3, and 4 have in common a mutation which prevents their growth on minimal medium, and that this primary effect is modified by the action of a number of other genes so that the various types differ qualitatively in their responses to phenylalanine, anthranilic acid, tryptophane, and nicotinamide. They therefore appear to be blocked at different steps along the biosynthetic pathway. Actually there are quantitative differences as well, for there is considerable variation within each type in the amount of growth produced on any substrate, as shown by the standard errors in table 1. It seems likely that if enough crosses were analyzed, a more or less continuous spectrum from type 4 to suppressed mutant or wild type would be indicated.

The analyses which have been made are not sufficiently extensive to permit definite conclusions as to the number of modifying genes involved or the precise effect of any of them. Such conclusions must await the accomplishment of a large amount of genetic work, coupled with enzyme studies. The present work clearly demonstrates, however, that one may be misled if one attempts to assign the basic effect of a genetic mutation to a particular biosynthetic step on the basis of growth response alone.

SUMMARY

A genetic analysis of several tryptophane- or nicotinic acid-utilizing strains of Neurospora has provided evidence that these strains have in common a mutation which prevents their growth on minimal medium, but that their responses to various growth substances are influenced by the action of a number of modifying genes. The influence of the modifiers is such that different strains which carry the same primary mutation appear to be blocked at different biosynthetic steps along the pathway which leads to the formation of tryptophane and nicotinic acid. A suppressor of the primary mutation has also been found.

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CONTRASTING TYPES OF POPULATION STRUCTURE IN DROSOPHILA*

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INTRODUCTION

As soon as it became apparent that the genus Drosophila provides unique opportunities for the study of speciation and evolutionary mechanics, the efforts of many investigators were concentrated on the clarification of the taxonomy and geographical distribution of the members of the genus. This turned out to be an enormous undertaking; the great diversity of "wild" species, largely uncharted during the early days of Drosophila genetics, has presented workers in this field with all the ancient and exacting problems of taxonomy and phylogeny, as well as many new ones. Such work is a necessary preliminary to the study of the more dynamic problems of evolution, which must start at the population level. These more intensive phases of the study—the close analyses of speciation patterns and population genetics of the various forms—until recent years have of necessity been held in abeyance. Now that a respectable body of taxonomic and distributional information exists, however, we may look forward to the development of what might be called the comparative evolution of the genus, based on quantitative population genetics. The purpose of the present discussion is to deal with certain aspects of such a comparative evolution.

When our present knowledge is viewed broadly, strongly contrasting population patterns are apparent. Thus, it is not legitimate to ask: "What is the structure of populations in Drosophila?"; there are many structures, not one. Some of the broad contrasts have been apparent for some time. For instance, the genus has its cosmopolitan forms, its weeds. *D. melanogaster, D. immigrans, D. busckii* and a number of others, are world-wide in distribution and their population patterns and structures are complexly interwoven with the activities of the human race. They display such phenomena as the cyclic occurrence of tremendous populations, often under strictly local conditions. Such populations may be annually decimated, as in the temperate climates, or they may fall less dramatically, as in the tropics. Association with man undoubtedly results in considerable transportation of individuals to all parts of the world, resulting in continual unpredictable admixtures. Because of this uncertainty, more emphasis has come to be placed on the study of species less affected by such factors.

Clearly distinguished from the above are large groups of species which show "natural" distributions and are much less affected by the activities

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of man. Such species, as for example, *D. pseudoobscura* of western North America, *D. robusta* of eastern North America, and *D. willistoni* and its relatives of South America are obviously successful and highly differentiated native faunal elements. Despite their disinclination to become ecologically associated with man, they nonetheless show considerable adaptability. The simple fact that many of them are easily reared in the laboratory attests to this adaptability.

A still greater contrast is supplied by a series of species, which again is not confined to any one of the natural taxonomic groups of the genus, which give every evidence of being delicately adjusted and highly specialized forms. They frequently show sharp ecological localizations and are often difficult to trap and to rear in the laboratory. As examples of this group we may cite such species as *D. floricola,* the larvae of which feed on the pollen of Datura and related flowers, or *D. inversa,* which apparently breeds exclusively in the froth produced by spittle-insects.

Although it is obvious that such species present problems and conditions not met with in the more commonly studied species of Drosophila, no analysis at the population level has yet been made of any of them. Such forms are very poorly known largely because they are difficult to obtain in numbers requisite to quantitative studies and because they are for the most part extremely difficult to rear in the laboratory with the usual methods.

Before a realistic comparison can be drawn between evolutionary patterns, considerable quantitative data on natural populations must be available. Relatively few species or species groups of Drosophila are sufficiently well known as yet to permit such comparisons but at least a beginning can be made. I have chosen to compare the pattern in *Drosophila robusta* with that apparent in the "wild" North American relatives of the domestic species *Drosophila virilis.* Such a comparison is favored by the fact that these flies occupy a roughly similar or at least broadly overlapping geographical area in the United States. Both include indigenous forms which are affected in only a minor way by the activities of man. At least a modicum of facts is known concerning the ecology of these forms. Although the American *obscura*-group and the *willistoni*-group of South America are perhaps better known in a number of ways, the kind of contrasts and comparisons I wish to draw are better illustrated by relatively distantly related forms which are sympatric.

POPULATION STRUCTURE IN DROSOPHILA ROBUSTA

Drosophila robusta is a characteristic inhabitant of the deciduous forest of the eastern United States. Its geographical distribution superimposes rather closely on that of the American Elm *(Ulmus americana),* the infected sap exudations of which serve as its principal breeding site. The species has been found as far south as northern peninsular Florida and south-central Texas. To the west it extends in the river valleys out onto the great plains, having been recorded as far west as the extreme northwestern

corner of Nebraska. On the north, it has been collected from Maine to Minnesota, and it probably occurs in southern Canada as well.

Within this area, *D. robusta* has only a single close relative. This is the poorly known species *D. colorata,* which has been recorded sporadically within the range of *D. robusta. D. colorata* has a widely different chromosome group from that of *robusta;* it has not been possible to hybridize the two (*colorata,* however, is very difficult to raise in the laboratory) and further, the salivary gland chromosome banding appears to bear no close resemblances in the two species. It is thus suggestive that *robusta* and *colorata* are highly differentiated, clear species of long standing. It is of interest to note that the only other known members of the *robusta* species group are found in China and Japan, a fact which recalls similar disjunct distributions of other elements of the flora and fauna of eastern North America. One may hazard the suggestion that *D. robusta* is an old and conservative inhabitant of the deciduous forest and that its history may well be closely allied with that of its principal host, the American Elm.

A number of the studies which have been made by Stalker and the writer on this species provide evidence as to the nature of its population structure. First, we have sampled populations from widely separated parts of its general range, and have studied both the distribution of relatively inverted segments of the chromosomes and inherited morphological differences (Carson and Stalker, 1947; Stalker and Carson, 1947). Both morphological characteristics and gene arrangement frequencies show gradual and continuous clinal changes over the range of the species. For instance, the Tennessee and Georgia populations have gene arrangement frequencies which are strikingly different from those of central Missouri, and the direction of the tendencies is continued as one proceeds northward into Iowa. On the other hand, the majority of the gene sequences occur very widely throughout the range of the species and it is only on the periphery that certain arrangements approach or reach fixation to the exclusion of their alternatives. Therefore, although the peripheral populations may be quite distinct from one another, they are interconnected by gradual and continuous clines. Morphological characteristics show the same type of clinal change. These morphological differences have been shown to be hereditary and the data complement the broad outlines of the cytological variability, although it has not been possible to show that specific inversions underlie the particular morphological characteristics measured.

Where ecological conditions change rapidly in a short linear distance, as on the slope of the Smoky Mountains, clines of morphological and cytological characteristics have also been found (Stalker and Carson, 1948). In some instances these clines are sharp, but again, there is a general continuity between valley and mountain populations. As expected, the clines do not parallel very closely the geographical ones.

Finally, we have studied the gene arrangements in a single population near St. Louis, Missouri, over a three-year period (Carson and Stalker, 1949). Frequency equilibria of the gene arrangements in this population

were maintained essentially unchanged from year to year. Slight significant shifts in frequency occur, some of which are reversed and recapture the former equilibria, but the general picture of equilibrium is borne out. Levitan (1951a) reports no seasonal change in the frequencies of gene arrangements in a population of this species at Englewood Cliffs, New Jersey. Near Blacksburg, Virginia, however, this author found significant changes in the frequencies of certain arrangements during the year as well as a difference in frequency of certain arrangements in males and females (Levitan, 1951b, c). Stalker and Carson (1949) showed that in the Missouri population there was a significant shift to a more "southern" phenotype during the summer; this shift has a genetic basis. Although the above cases are suggestive, it is still questionable whether they represent regular, repeated cyclical changes with season such as have been demonstrated in some populations of *D. pseudoobscura* by Dobzhansky (1943).

A certain amount of information bearing on population structure from the ecological point of view is now available for this species (Carson and Stalker, 1951). Infected sap exudations, or "slime fluxes" of deciduous forest trees, especially elms, have been shown to constitute the primary natural breeding site of this species. The proper microbiological conditions for oviposition of *robusta* females appear to be quite critical and are by no means present on every slime flux. As fluxes are by no means ubiquitous, it is implicit that the motility of the species must of necessity be great to enable ovipositing females to successfully reach favorable spots.

Discovery of the breeding site of *D. robusta* helps to explain its microecological distribution. It has been known for some time, for instance, that the species is almost wholly absent from coniferous forests, although in deciduous areas it may be caught equally well on upland or lowland, and is quite common in suburban and park-like environments. It successfully invades rather open orchard areas, where it breeds on the gummy exudations of peach, cherry and plum (Prunus) trees, rather than on the fruit. Oak hillsides have been notoriously poor for this species and it may well be that the records of it breeding on alcoholic exudations of *Quercus alba, Q. palustris* and *Q. rubra* are somewhat exceptional and represent a less well-mastered ecological niche for the species.

Population density and dispersal rates have not been determined for *D. robusta,* although it may not be amiss here to mention a few minor experiments which have been done, especially to test motility. A single cup of fermenting banana mash was set under a beach umbrella in the center of a large plowed field which had been recently planted with small tomato plants. The field had been cultivated just prior to the experiment and there were practically no weeds. The shortest distance from the trap to shrub cover was 110 feet. During the day there were no flies in the trap and the field was in the hot sun and swept by strong northwest winds. Nevertheless, in two evening collections, 13 specimens of *D. robusta* were captured, proving that this species easily flies across a considerable open space.

In another series of experiments, several traps were hung among a group of shrubs at the edge of a country lawn, beyond which were open wheat fields. Flies were captured morning and evening, marked and released without feeding at varying distances from the traps. Of 362 flies so marked, 23, or 6.4 per cent, returns were recorded. Twelve of the returns were from release points 400 feet or more from the traps. One male returned three times from distances of over 400 feet. Two returns were obtained of flies released across open wheat fields, one a distance of 600 feet and another 1850 feet, or over a third of a mile. Most of the returns were after an elapsed period of 24 hours, although in one instance a fly was caught an hour and a half after being released 400 feet away. Such evidence as there is thus indicates a high degree of motility in this species. Before this impression can be confirmed, however, a release experiment comparable to those performed with *D. pseudoobscura* (Dobzhansky and Wright, 1943, 1947) and *D. willistoni* (Burla, et al., 1950) will be necessary.

Little is known concerning breeding season and overwintering for any species of Drosophila, although the effect of such factors on the structure of natural populations is obvious. Carson and Stalker (1948) have been able to show that females in the fall population of *D. robusta* near St. Louis, Missouri, consist almost exclusively of non-breeding individuals. Females captured from the middle of September on are characteristically virgin (95 per cent), have minute ovaries and disproportionately large quantities of body fat. This condition has been shown to be accompanied by a state of reproductive diapause, which is broken only slowly by laboratory conditions. The first flies in the spring are invariably very dark, battered individuals which have obviously overwintered as adults. This fact, together with the fact that few if any young flies are captured until there has been an opportunity for the completion of a spring generation, indicate that most, if not all, overwintering stages are adults. The fact that the fecundity of spring-caught females is very high suggests that the height of the breeding season is reached early in the year, by perhaps the first of July in the latitude of St. Louis.

The overall picture which emerges for *D. robusta*, then, is one of a wide-ranging, motile species showing gradual clinal distribution of genetic characteristics. These clines are not stepped and do not reach levels of fixation such that one would be tempted to erect subspecific designations. As a species, it is isolated; its only close relative is widely different. There is a high degree of heterozygosity for gene arrangement, especially in the central part of the range, and this grades off in homozygosity at the periphery. All indications thus point to a relatively large, undivided and continuous gene pool which permits considerable gene flow into all parts of the population. This does not mean, of course, that the entire species is one panmictic population; isolation by distance effectively prevents this at any one time level, but discrete, strongly isolated subpopulations do not appear to occur. The obviously large effective size of interbreeding populations, although not technically measured, is attested to by the clinal phenomena and the considerable number of individuals which successfully

overwinter. There is no evidence of the formation of small populations of a size conducive to the operation of genetic drift, either seasonally in the populations studied, or as reflected in any of the geographical studies of the species. These latter considerations, however, should not be construed to mean that ecological "island" populations may not be discovered in the future, but the species appears to be generally otherwise characterized.

POPULATION STRUCTURE IN THE "WILD" RELATIVES OF *Drosophila virilis*

The painstaking work of Patterson, Stone and Griffen (1940, 1942), Stone and Patterson (1947), Patterson (1952), Hsu (1952) and others of the Texas group has uncovered a fascinating and extraordinarily complex situation among the native North American species related to the domestic *D. virilis*. With the exception of *D. virilis* itself, these species show natural distributions; they are obviously, like *D. robusta*, indigenous forms of wide distribution.

The elucidation of this group has been a difficult undertaking. It has become increasingly clear that, unlike *D. robusta*, there are a relatively large number of very closely related taxonomic entities among the wild members of this group. These entities have been generally regarded as falling into two groups which are phylogenetically somewhat separated, designated as the *americana* complex and the *montana* complex. The former complex includes about four recognized entities (Hsu, 1952): 1) *D. americana americana*, the eastern branch (Ohio River valley and the northeast); 2) *D. americana americana*, western branch (Missouri River valley northwest to Montana); 3) *D. americana texana* (southeastern United States) and 4) *D. novamexicana* (New Mexico, Arizona and Colorado). The *montana* complex at present consists of four entities: (Patterson, 1952): 1) *D. montana* (Rocky Mountains; Sierra Nevada northwest to Washington); 2) *D. flavomontana* (Rocky Mountains); 3) *D. lacicola* (Minnesota and Wisconsin) and 4) *D. borealis* (Minnesota, Wisconsin and one locality each in Idaho and Colorado).

The central fact which stands out in the comparison of this situation with that found in the *robusta* group is that within the geographical range which is occupied by the single entity *D. robusta*, one finds four or possibly five entities of the *americana-montana* complexes. The postglacial occupation of northeastern North America by flies of these two groups thus shows rather striking differences. *Robusta* has reoccupied the glaciated area without pronounced local differentiations. Wild *virilis*-group flies, on the other hand, have undergone considerable specific, subspecific and possibly also local populational differentiation. In the following discussion some factors which may be responsible for these differences will be suggested.

First, there appear to be significant and important differences between *robusta* and wild *virilis* flies in the structure of their populations. Perhaps the greatest technical problem in connection with studies of the wild *virilis* complexes has been the general inability to catch them in large numbers.

Ordinarily, rather few specimens are obtained in banana traps, although the occasional large collections which have been made indicate that this bait attracts the flies well. *Robusta,* on the other hand, can usually be collected in adequate numbers almost anywhere within its range by this method. This difference in ease of collection is probably the principal reason why quantitative studies of wild populations of the flies of the *americana-montana* complexes have not so far been possible. The multiplicity of forms, furthermore, have posed many important problems of taxonomy, phylogeny, comparative cytology and sexual isolation, and attention has largely been centered on these rather than on intrapopulational phenomena.

What has been a serious technical stumbling block to the intensive study of these flies may well reflect one of the most interesting and significant features of the group. The question may be asked: Is the difficulty of collecting specimens of wild *virilis* due to the fact that these flies are truly very rare and thus exist only in small populations or is something the matter with the techniques of collection? In the last several years, evidence has been accumulating which indicates that ability to collect these flies depends on a number of things, most of which are ecological in nature. These factors reflect what appears to be a profound difference between the members of this group and the *robusta* group.

For a long time it has been known that *americana-montana* flies are rarely captured except closely adjacent to water. Actually, it has been found desirable to place traps right at the water's edge. The best collections which have been made to date have been made in such situations under conditions of high humidity. This suggests, of course, that the flies are ecologically restricted in some way, but until the discovery of Spieth (1951) no real clue as to the details existed. In collections made at Lake Itaska in Minnesota, Spieth observed the usual localization of wild *virilis. Montana*-group flies could be captured in banana traps only closely adjacent to the water. If the traps were moved back only 30 feet from the water, they yielded no *montana* group, although good catches were obtained at the water's edge. *Robusta,* which was found breeding on elms, was caught equally well at both locations.

Spieth found *D. borealis,* not *D. lacicola* as was reported (Wheeler, in litt.; see also Hsu, 1952) in the rotting phloem of felled aspen trees *(Populus tremuloides)* which had previously been inundated by high water. This breeding site suggests the nature of the ecological restriction of this group of flies, and coupled with their apparent disinclination to disperse away from the water's edge, this fact appears to supply an important clue to the population structure of wild *virilis.* The obvious surmise that, outside the range of the aspen, the relationship may be to other riparian trees, especially Salicaceae, has been borne out by several unpublished observations made since Spieth's discovery. Thus Wheeler (in litt.) reports that *D. montana* has been found breeding on aspen and alder *(Alnus sp.)* and *D. flavomontana* on narrow-leaved cottonwood *(Populus angustifolia).* Blight and

Romano (unpublished) located larvae and large numbers of pupae of *americana-complex* flies on previously submerged stumps and trunks of the sandbar willow (*Salix interior*) on the bank of the Meramec River near St. Louis, Missouri. Traps placed near these trees yielded exceptionally large numbers of *americana-complex* flies.

On these preliminary observations, one may hazard a suggestion as to the probable nature of natural populations in this group. One may visualize relatively small populations, building up extremely locally under favorable conditions. More importantly, the disinclination of the flies to disperse away from the water would guide the differentiation of these populations in a linear fashion along watercourses, unlike the more diffuse structure in *robusta*. Whether the apparent low motility of the flies away from water equally applies to the linear migration of flies along streams is not known, but the situation would seem to call for a differentiation of disjunct, semi-isolated local breeding units.

It is tempting to suggest that the most stable environment would be something in the nature of a beaver dam or workings, where the host species of the flies (aspen, willow or alder) is cut naturally by the beavers and incorporated in contact with the water in a regular and abundant fashion. The flood plains of rivers, especially in the central United States, present a rugged, shifting environment. Periodic floods would certainly provide plenty of submerged and re-emerged driftwood, as well as subject the riparian trees to influences which might give rise to rotting phloem *in situ* on live specimens. The major point, however, is that such habitats would be confined to the flood plains and so would impose upon the species of Drosophila breeding there a fundamentally linear distribution.

CONCLUDING STATEMENT

Strong contrasts between the wild members of the *virilis* group and *D. robusta* are apparent. Although sympatric, these forms show differences in their fundamental ecological differentiation. *Robusta*, with only one not very close relative, is distributed widely and shows gradual clinal variation. Its connection with the American Elm is inescapable, and much of its population structure seems to be built around this fact. It is commonly found in upland and lowland under natural conditions, and it successfully invades suburban and urban areas as well as disturbed areas such as orchards, where it is able to adopt new hosts in the form of various exotic tree species. Its genetic differentiation fits well into this general picture; such a habitat would not call for stepped clines or sharp evolutionary differentiation under local conditions, yet gene flow is of course not so great that it swamps the clinal variation.

Members of the wild *virilis* group are numerous and very closely related, indicating recent and rapid speciation. They are differentiated geographically in a linear fashion, following river and stream valleys. This appears to reflect the peculiar and quite specialized natural breeding site, the rot-

ting phloem of riparian trees, apparently of only certain species. The sensitivity of the group to low humidity and their apparent low migratory ability (except possibly up and down watercourses) should lead, in contrast to *D. robusta,* to the occurrence of relatively discontinuous populations, distributed in a linear fashion. The microstructure of populations in none of the species of the *americana-montana* complexes has as yet been sufficiently studied to indicate whether the genetic variability fits the above hypothesis. The situation in wild *virilis* certainly contains, quite unlike *robusta,* all of the ingredients conducive to the formation of populations of a size in which genetic drift could play a role, and the suggestion has been made several times before that this phenomenon may have been important in the history of this group. If such is the case, it is not unlikely that at the present time conditions are sufficiently similar that a quantitative study of the genetic structure of populations in these forms would reveal the presence of drifting conditions in existing local populations. It is much to be hoped that the new ecological information on *robusta* and the wild *virilis* complexes will contribute to an increasingly clear understanding of the striking differences in evolutionary pattern between them.

SUMMARY

The known facts concerning population structure in the single species *Drosophila robusta* and the many "wild" members of the *Drosophila virilis* species group, both of which are widespread in North America, are reviewed and discussed. Although the information is incomplete, the suggestion is made that the recent and rapid speciation in the *virilis* group, as contrasted with the much more conservative tendencies of *D. robusta,* has been conditioned by the close ecological restriction of the former to a riparian habitat which imposes on the species of this group a fundamentally linear distribution, following river valleys. Populations of these species may be viewed as being relatively discontinuous, due to the nature of the habitat and the apparent low motility of the flies. *D. robusta,* on the other hand, displays strongly contrasting features of population structure which appear to be less conducive to speciation. So far as is known, the patterns of genetic variability within the compared forms fit the above hypothesis.

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LETTERS TO THE EDITORS

Correspondents alone are responsible for statements and opinions expressed. Letters are dated when received in the editorial office.

"GENE" AND "GENETICS"

As a science comes of age, its basic terminology may become so well established that the origins of some of the most frequently used words are forgotten by or even unknown to many who use those words daily. This fact occasionally leads to some misconceptions or at least to misstatements.

In a recent elementary textbook in genetics[1] we find the statement, "Johanssen (*sic!*) also coined the word 'gene,' from which has been derived the word "genetics." That the word "gene" was coined before the word "genetics" has also been suggested in Grobman's[2] semi-popular book on radiation genetics. Grobman writes, "Such a factor has been called a gene (hence the science, genetics)." Do these statements reflect the correct sequence of events?

The word "genetics" seems to have been introduced by the late William Bateson[3] in his inaugural address to the Third Conference on Hybridisation and Plant-breeding in 1906. Bateson pointed out that with the rediscovery of Mendel's laws the study of hybridization and plant-breeding became a developed science, but also compelled the adoption of a terminology, "which, if somewhat deterrent to the novice, is so necessary a tool to the craftsman that it must be endured." He further pointed out that "the science itself is still nameless, and we can only describe our pursuit by cumbrous and often misleading periphrasis." He then made the following proposal. "To meet this difficulty I suggest for the consideration of this Congress the term *Genetics,* which sufficiently indicates that our labours are devoted to the elucidation of the phenomena of heredity and variation: in other words, to the physiology of Descent, with implied bearing on the theoretical problems of the evolutionist and the systematist, and application to the practical problems of breeders, whether of animals or plants." Incidentally, it might be pointed out here that this conference was held in London and not in Paris, as stated in Babcock and Clausen[4]. The fourth genetics congress, held in 1911, was in Paris. In another paper written about the same time, Bateson[5] used such terms as "allelomorph," "factor," "determiner," and "character," and referred to Johannsen's pure-line work, but made no reference to the word "gene." This omission would tend to indicate that the word had not been proposed at that time.

In 1909, Johannsen[6] in the first edition of his "Elemente" pointed out that there was no satisfactory term for the "something" in the gametes and zygote which determines or very substantially influences a character in an organism. The very ambiguous term, "Anlage" was usually used,

but there were also many other terms most of which had the disadvantage of being connected with definite hypotheses. He pointed out that Darwin's "Pangene" might be used but objected to it on the ground that it was a compound word and he proposed the latter half, "das Gen," as a substitute. This word had the advantage of no previous connotation and also expressed the significant idea of Darwin's term. From Johannsen's statements it is clear that this word was being proposed there for the first time.

The first reference in the English language to Johannsen's "Gen" was in a paper by G. H. Shull[7] which appeared during the same year. Shull made the statement that Johannsen coined the word as a "substitute for pangenes, ids, allelomorphs, etc.," which would indicate that in 1909 he considered that Johannsen had first proposed the term. Incidentally, it was Shull who introduced the anglicized spelling, substituting "gene" for the German "Gen." Further comments on the spelling of "gene" were made by Shull[8] in 1912 and again in 1915 (Shull[9]) in his discussion of definitions in the "New Standard Dictionary."

Although the point here is only of minor importance, it seems desirable for the sake of the record to point out that "genetics" was not derived from "gene" but preceded it.

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MARCH 13, 1952

INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE; PROPOSED AMPLIFICATION CLARIFICATIONS AND EXTENSIONS TO BE CONSIDERED BY THE INTERNATIONAL CONGRESS OF ZOOLOGY, COPENHAGEN, 1953

Zoologists and paleontologists are reminded that at its meeting held in Paris in 1948 the Thirteenth International Congress of Zoology decided that a number of general problems of great importance involving the text of the International Code of Zoological Nomenclature should be brought forward for decision at the next (Fourteenth) International Congress of Zoology at its meeting to be held in Copenhagen in 1953. The Paris Congress further decided that, as a preliminary to the submission of these problems to the Copenhagen Congress, the secretary to the International Commission on Zoological Nomenclature should confer with interested specialists and, having done so, should submit comprehensive reports, with recommendations.

In pursuance of the duties so entrusted to me, I have prepared papers on each of the problems remitted to me for report, in each of which I have set out the issues on which, as it appears to me, the Copenhagen Congress will need to take decisions. In these papers also I have submitted for consideration a number of suggestions based upon such preliminary consultations as it has already been possible to hold. The object of these papers is to elicit expressions of opinion on the issues involved from as wide a circle as possible of interested specialists.

The subjects dealt with in the papers referred to above are the following:

(1) Emendation of zoological names: proposed substitution for Article 19 of simple clear-cut rules capable of being easily applied (commission's reference Z.N.(S.)356);

(2) Clarification and amplification of the rules relating to the naming of families and lower categories of suprageneric rank (commission's reference Z.N.(S.)357);

(3) Proposed introduction of rules for regulating the naming of orders and higher taxonomic categories (commission's reference Z.N.(S.)360);

(4) Species to be accepted as the type species of a nominal genus, the name of which was published in a generic synonymy, if names so published are to be treated as possessing nomenclatorial availability (Z.N.(S.)387);

(5) Application to be given to a trivial name which, when first published, was applied to a particular species or specimen but which is stated also to be a substitute name for some previously published name (commission's reference Z.N.(S.)361);

(6) Neotypes: question whether this class of type specimen should be officially recognized and, if so, under what conditions (commission's reference Z.N.(S.)358);

(7) The means to be devised for securing stability in zoological nomenclature (commission's reference Z.N.(S.)359).

A special volume (vol. 7) of the *Bulletin of Zoological Nomenclature* has been allotted for the publication of the foregoing papers, which, it must be understood, constitute an important instalment of the Agenda

on nomenclature questions of the Copenhagen Congress next year. Parts 1 and 2 containing the first instalment of the above papers will be published on 25th February 1952; the whole of the remainder of the volume will be published within the next six weeks.

The object of the present notice is to draw the attention of zoologists and paleontologists to the arrangements being made for the consideration of the foregoing problems by the Copenhagen Congress next year, and to express the hope that nomenclature committees of museums and other scientific institutions and also as many individual specialists as possible will furnish as soon as possible answers to the questions specifically asked in the concluding paragraph in each of the seven papers enumerated above regarding the action which, in their opinion or, in the case of committees, in the opinion of their members, it is desirable that the Copenhagen Congress should take on each of the important problems involved. It is particularly hoped that there will be a wide and representative response to the present appeal, so that the proposals to be submitted to the Copenhagen Congress may be such as will command the widest possible measure of support among the general body of zoologists and paleontologists, both those engaged on taxonomic work and also those engaged in the teaching of zoology and geology and those working in the various fields of applied biology.

Nomenclature committees and individual specialists who respond to the present appeal for assistance and advice will render a double service if they will be so good as to assist the International Commission by observing the following procedure when furnishing statements of their views: (1) Where comments are furnished on two or more of the general problems enumerated above, the comments furnished on each of those problems should be on separate sheets of paper. (2) Every comment furnished should be clearly marked with the commission's reference number as indicated in the list given above. (3) Comments should be typewritten, on one side of the paper only, with wide margins and should be furnished in duplicate.

In order that there may be sufficient time to prepare the reports called for by the Paris Congress—and thus to make those reports available well ahead of the Copenhagen Congress—it is particularly hoped that nomenclature committees and individual specialists responding to the present appeal be so good as to dispatch their comments as promptly as possible.

All communications relating to the foregoing matters should be addressed to myself, as Secretary to the International Commission on Zoological Nomenclature (28 Park Village East, Regent's Park, London, N.W.1., England).

FRANCIS HEMMING
Secretary to the International Commission on Zoological Nomenclature

26 April 1952

A NEGLECTED ARTICLE OF LUTHER BURBANK

Luther Burbank in 1909 published an article entitled "Another Mode of Species Forming" (Burbank, L., Amer. Breeder's Assoc. 5, 40–43, 1909) which never attracted attention, judging by lack of reference to it in the horticultural literature. The significance of this article on the production of fixed hybrids between widely different species of horticultural plants would seem to be attested to by the fact that McFadden and Sears[1], in their studies on "fixed hybrids" (allopolyploids) in the wheats, gave reference to it. Burbank's article has been hidden so long and has such significance to horticulturists and plant breeders that it ought either to be reproduced or attention called to it in some well-known journal to reach all interested scientists. Many plant scientists would enjoy knowing that Burbank was the first to announce the production and singular behavior of fixed hybrids (allopolyploids). Also many even today have not caught the significance of Burbank's insistence that large populations are necessary to establish the potential merits of segregation from crosses. Another aspect is that of maternal inheritance in reciprocal crosses—apparent, imaginary or real.

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E. M. HILDEBRAND

COLLEGE STATION,
TEXAS
FEBRUARY 27, 1952

PUBLICATIONS RECEIVED

THE AMERICAN NATURALIST is glad to acknowledge here the receipt of books on biological and natural history subjects which are likely to be of interest to our readers. No undertaking to publish reviews is implied in this acknowledgment. Books for notice may be sent to:

EDITORIAL OFFICE
The American Naturalist
635 W. 247 St.
New York 71, N. Y.

Caullery, Maurice, 1952. Parasitism and symbiosis. 340 p., ill. $5.50. The Macmillan Company, New York.

Biologists in English-speaking lands will be grateful for this translation of the work of the dean of French zoologists. In a simple but masterful way, Professor Caullery summarizes an enormous wealth of data, some of it recently discovered and much more that has lain buried in special monographs rarely read by most general biologists, on parasitism, commensalism, and mutualism, chiefly in animals and particularly among water-dwelling invertebrates. The reader will have to provide his own interpretations of the facts described in terms of the modern theories of evolution. But evolutionists, perhaps more than other biologists, need to be constantly reminded about the stupendously varied and often bizarre forms which life takes, especially in the oceans and in the jungles, the existence of which is easily forgotten in the environment of modern laboratories.

T.D.

Fox, Sir Cyril S., 1952. Water, a study of its properties, its constitution, its circulation on the earth, and its utilization by man. 148 p., 25 plates, 4 text-figures. $8.75. The Philosophical Library, Inc., New York.

For a price that most readers will find unreasonably high, this book gives a very readable discussion of the topics indicated in its title, a profusion of useful statistical data and estimates, and 25 photographs.

T.D.

Goldschmidt, Richard B., 1952. Understanding heredity. An introduction to genetics. 228 p., 49 figs. $3.75. John Wiley and Sons, Inc., New York.

This discussion of the elementary principles of genetics is addressed to two classes of readers: first, to college students not intending to be biol-

ogists, and second to that anonymous group, the public. Because of the detailed machinery required to explain the mechanism of reproduction and heredity it will probably appeal more to the first than the second. In spite of the association of the author's name with denials of the existence of the gene, his book is a thoroughly orthodox treatment of the classical theory, clearly and, in general, simply written.

L.C.D.

Grüneberg, Hans, 1952. The genetics of the mouse, 2nd Ed., revised and enlarged. 650 p., 16 plates, 96 text figures. Martinus Nijhoff, The Hague.

This is a new, revised and considerably expanded edition of this standard review of mouse genetics. It is an admirable example of a synthetic review in which the original literature is listed and quoted (bibliographic references now number 1751 including the literature up to spring, 1951) together with suggestive or alternative interpretations by the author in many of the cases. There is a section on mutation induction, one on the genetics of cancer, one on gene action, a chapter on care and breeding of mice for experiments, a list of gene symbols, and a full index.

L.C.D.

Hooper, Emmet T., 1952. A systematic review of the harvest mice (genus Reithrodontomys) of Latin America. 220 p., gazetteer of localities of Latin America from which specimens were obtained, 29 p., literature cited, 7 p.; 9 plates illustrating crania; 24 text figures, 12 maps; paper, $4.00; cloth $4.60. Miscellaneous publications No. 77, University of Michigan Press, Ann Arbor.

A detailed and thorough taxonomic study, with evolutionary discussion. The paucity of natural history data reflects our ignorance of the biology of tropical American mammals, which can hardly be remedied until these background taxonomic studies have been carried through.

M.B.

Mann F., Guillermo, 1951. Esquema ecologico de selva, sabana y cordillera en Bolivia. 236 p., ill. Publication No. 3, Instituto de Geographia, University of Chile, Santiago.

The forests, savannahs and mountains of Bolivia represent the major tropical American landscape types. They are described in this book in terms of observations and impressions, with special reference to the adaptations of conspicuous animals. The ecological vocabulary sometimes seems forced, serving to hide our essential ignorance of the dynamics of these tropical biotas, but the treatment gives a useful perspective on the ecological diversity of a tropical region and brings out many stimulating and suggestive ideas. Each short section has an adequate summary in English and German.

M.B.